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Functional Organization of the Ventral Spino-Cerebellar Tract in the Cat

II

Connections with Muscle, Joint, and Skin Nerve Afferents and Effects on Adequate Stimulation of Various Receptors

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Contents

General Introduction 5

Methods 8

Nomenclature 9

Chapter I. *Identification and general behaviour of VSCT units* 10

Results 10

A. Method of identification. Localization of VSCT units 10

B. Antidromic stimulation 12

C. Behaviour on stimulation of muscle nerves 13

D. Resting behaviour 16

Discussion 17

Summary 19

Chapter II. *Characteristics of impulse transmission from Ib afferents to VSCT neurons* 20

Results 20

A. Susceptibility to asphyxia and anaesthesia 20

B. Decay of subliminal excitatory Ib action. Inhibitory Ib action 22

C. Effect of antidromic stimulation and ability to follow high repetition rates 27

D. Post-tetanic potentiation 29

Discussion 32

Summary 35

Chapter III. *Pattern of convergence of excitatory and inhibitory Ib effects onto VSCT neurons* 37

Results 37

Discussion 45

Summary 47

Chapter IV. *Effects on electrical stimulation of muscle, joint, and skin nerves* 48

Results 48

1. Mass discharge recording 48
2. Single unit recording 61
   A. I-units 61
   B. E-units 65
3. Facilitation evoked on stimulation of the dissected contralateral half of the spinal cord 68

Discussion 70

Summary 71

Chapter V. *Effects on adequate stimulation of various receptors* 72

Results 72

1. Adequate stimulation of muscle receptors 72
   A. Effects from muscles without, or with only weak, Ib connection to the investigated neuron 73
   B. Effects from muscles with strong Ib connection to the investigated neuron 77
   C. Units with aberrant behaviour 81
2. Adequate stimulation of cutaneous receptors 83
3. Adequate stimulation of receptors in deep structures 92
4. Effects displayed on mass discharge recording . . . 93

Discussion 94

Summary 99

Comments 100

General Summary 103

References 105

General Introduction

Only two spinal tracts ascend from the caudal part of the spinal cord to reach the cerebellar cortex without synaptic interruption, *viz.* the dorsal and ventral spino-cerebellar tracts. The dorsal spino-cerebellar tract (DSCT, Flechsig's tract) has been extensively investigated. The cells of origin constitute Clarke's column and the fibres ascend ipsilaterally in the dorsal part of the lateral funiculus to reach the cerebellum through the restiform body. The functional organization of the DSCT has been analysed in a series of investigations (GRUNDFEST and CAMPBELL 1942, LLOYD and MCINTYRE 1950, LAPORTE, LUNDBERG, and OSCARSSON 1956 a, b, LAPORTE and LUNDBERG 1956, LUNDBERG and OSCARSSON 1956, HOLMQVIST, LUNDBERG, and OSCARSSON 1956). The DSCT neurons have been shown to be monosynaptically activated from muscle spindle and Golgi tendon organ afferents. Experiments with adequate stimulation of stretch receptors in muscles have confirmed that the tract conveys information from muscle proprioceptors.

The ventral spino-cerebellar tract (VSCT, Gowers' tract) has been much less investigated. Anatomical studies on this tract have recently been reviewed by YOSS (1953), JANSEN and BRODAL (1954), and CARREA and GRUNDFEST (1954). References to older literature can be found in MACNALTY and HORSLEY (1909) and BECK (1927). The anatomical data of the VSCT are partly incomplete. The cells of origin have not been conclusively determined (cf. SPRAGUE 1953, JANSEN and BRODAL 1954). It is, however, generally agreed that at least most of the VSCT axons immediately after their origin in the grey matter cross to the other side of the spinal cord. The axons then ascend in the peripheral part of the ventro-lateral quadrant of the spinal cord,

as most recently described by Yoss (1953). The VSCT continues through the medulla oblongata up to the pons where it loops up over the superior cerebellar peduncle to enter the cerebellum. Most of the VSCT fibres terminate in the anterior lobe.

The first attempt to analyse the VSCT with electro-physiological methods was made by CARREA and GRUNDFEST (1954). These authers recorded a mass discharge from the superior cerebellar peduncle on electrical stimulation of various nerves. This discharge, which had a long duration (tens of msec) and could be elicited from ipsilateral and contralateral muscle and skin nerves, was attributed to activity in the VSCT. The conduction velocity of the fastest fibres contributing to the discharge was assessed to about 80 m/sec.

The next electro-physiological study of the VSCT was made by HOLMQVIST and OSCARSSON (1956) and OSCARSSON (1956). They obtained results differing from those found by CARREA and GRUNDFEST and it was concluded that the discharges recorded by the latter authers could not have been due to activity in the VSCT. The VSCT mass discharge was identified by recording from the surface of the superior cerebellar peduncle where the tract is isolated from other ascending spinal tracts. An appreciable discharge was only recorded on stimulation of contralateral muscle nerves. The discharge had a duration of a few msec and appeared on increasing stimulation with the Ib component (BRADLEY and ECCLES 1953, ECCLES, ECCLES, and LUNDBERG 1957 a, LAPORTE and BESSOU 1957) of the ingoing volley indicating that it was due to excitatory action from Golgi tendon organ afferents. The delay of the discharge at different levels of the spinal cord showed that the transmission from the primary afferents to the tract neurons was monosynaptic and that the fastest fibres had a conduction velocity of about 120 m/sec. The VSCT was found to be completely or almost completely crossed and the DSCT completely or almost completely uncrossed. This was favourable as it permitted the VSCT mass discharge to be recorded from the dissected spinal cord in isolation from the DSCT discharge. This method of recording greatly facilitated the present study and was exclusively used in an investigation concerning the primary afferent collaterals and

spinal relays of the dorsal and ventral spino-cerebellar tracts (OSCARSSON 1957 a).

The aim of the present investigation has been to further elucidate the organization of the synaptic connections between primary afferents and VSCT neurons, and to obtain information concerning the functional significance of these connections by studying the response of the tract neurons on adequate stimulation of various receptors.

Chapter I deals with identification of single VSCT units with the micro-electrode technique. The previous result showing that the VSCT is monosynaptically activated from contralateral Golgi tendon organ afferents is used for identification of the tract neurons. In this chapter it is shown that two types of VSCT units exist and can be distinguished on supramaximal stimulation of muscle nerves.

In Chapter II characteristics of the impulse transmission from Golgi tendon organ afferents to tract neurons and in Chapter III the pattern of convergence of excitatory and inhibitory Ib effects onto VSCT units are described.

Chapter IV is concerned with effects in the VSCT evoked on electrical stimulation of other afferents than Ib afferents. It is shown that strong effects from high threshold muscle and joint nerve afferents and low and high threshold skin nerve afferents converge onto the VSCT neurons from an extensive receptive field. In Chapter V, finally, attempts are made to evaluate the functional significance of the convergence of effects from the different types of primary afferents. The results indicate that the connection with Golgi tendon organ afferents is of little, or no, functional significance and suggest that the VSCT is a pathway forwarding exteroceptive information.

Methods

The experiments were performed on cats under nembutal anaesthesia (40 mg/kg intraperitoneally) or on not anaesthetized decerebrate cats. The decerebration was performed under ether anaesthesia and recording usually began about two hours after the interruption of the anaesthesia. The hindlimbs were denervated and some of the severed nerves mounted for stimulation in pools of warm mineral oil. The spinal cord was usually transected in the upper thoracic region and then, after removing the dorsal columns for some centimetres in caudal direction, divided medially. One or both of the dissected spinal halves (except dorsal columns) were mounted for recording in a pool of warm mineral oil (cf. LAPORTE et al. 1956 a, OSCARSSON 1956, 1957 a). A laminectomy was performed at the L I region for micro-electrode recording and another laminectomy in the lower lumbar region for judging the ingoing volley. The rectal temperature was held within 36.0—39.0°C. A high room temperature of about 29° C and pools of warm mineral oil diminished the risk of local cooling. Further methodological data for certain of the experiments are given in Chapters I and V.

The electrical stimuli were condensor discharges of short duration (about 50 μsec at the 50 per cent level). These stimuli, at the maximal strengths used, were supramaximal for the A fibres but subliminal for at least the majority of the C fibres. *Supramaximal* will be used to denote supramaximal for A fibres.

For details concerning the micro-electrode technique see LAPORTE et al. (1956 b).

Nomenclature

In this paper *tract* is used to denote a bundle of nerve fibres having the same origin, function, and termination, whereas *fasciculus* is used to denote a subdivision of the funiculi of the spinal cord containing fibres to more than one tract (cf. e. g. DORLAND 1947, LARSELL 1951). It is proposed that Flechsig's tract and the dorsal spino-cerebellar tract (DSCT) and similarly Gowers' tract and the ventral spino-cerebellar tract (VSCT) should be used synonymously. Flechsig's fasciculus is used to denote the dorsal part of the lateral funiculus containing among other tracts the dorsal spino-cerebellar tract (cf. LAPORTE et al. 1956 a), and Gowers' fasciculus the area occupied by the ventral spino-cerebellar, the lateral spino-thalamic, the spino-tectal, and possibly other tracts.

Ia and *Ib afferents* are used synonymously with group I muscle spindle and Golgi tendon organ afferents.

Ipsilateral and *contralateral* refer to the site of recording from the tract or fibre in the tract.

Supramaximal stimulation is used to denote stimulation supramaximal to A fibres (see Methods).

Chapter I

Identification and general behaviour of VSCT units

It has previously been reported (OSCARSSON 1956) that a mass discharge in the VSCT appeared on stimulation of contralateral muscle nerves. No appreciable discharge appeared on stimulation of skin nerves or ipsilateral muscle nerves. From experiments in which the mass discharge was related to the ingoing volley in the primary afferents, it was suggested that the mass discharge was due to excitatory action from Golgi tendon organ afferents.

For the further analysis of the synaptic connections to the VSCT neurons it was desirable to record from single units. The present chapter deals with identification of VSCT fibres with the micro-electrode technique. VSCT neurons will be shown to receive excitatory action from Ib afferents but no appreciable effects from Ia afferents. Two types of VSCT units, distinguished on supramaximal stimulation of muscle nerves, and their resting behaviour, will be described.

RESULTS

A. *Method of identification. Localization of VSCT fibres*

The search for VSCT units was performed with an arrangement similar to that used by LAPORTE et al. (1956 b) when investigating single units in the DSCT. The localization of the VSCT at a superficial region of the ventro-lateral quadrant of the spinal cord made some modification necessary. The whole preparation was rotated around its longitudinal axis for about 20 degrees. This made the micro-electrode, when inserted vertically, traverse the VSCT along its greatest transectional extension as shown in the diagram in Fig. 1. Before the micro-

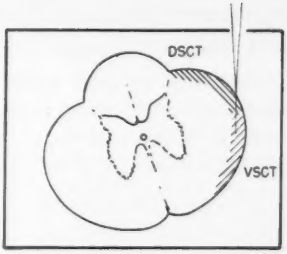


Fig. 1. Diagram to show arrangement used on search for VSCT fibres. Preparation rotated about 20 degrees which permits the microelectrode, when inserted vertically, to traverse the VSCT along its greatest transectional extension. The hatched areas indicate the approximative localizations of DSCT and VSCT.

electrode reaches the VSCT, the lateral part of Flechsig's fasciculus is passed through. The electrode was usually inserted during continuous stimulation of muscle nerves at a rate of about 10 stimuli per second. The strength was adjusted to be slightly supramaximal to group I afferents. This procedure did not seem to have any adverse effect on the preparation as no change in behaviour of the encountered units was observed even after hours of such stimulation.

Two categories of neurons were found in the lateral funiculi which responded on stimulation of group I muscle nerve afferents. There were encountered, in the dorsal part of the lateral funiculus, DSCT fibres activated from ipsilateral muscle nerves, and in the ventral part, VSCT fibres activated from contralateral muscle nerves. In some experiments the microelectrode was inserted during continuous stimulation of the ipsilateral and contralateral hamstring nerve. In spite of the fact that in these experiments only the lateral part of Flechsig's fasciculus was traversed (cf. Fig. 1) usually more DSCT than VSCT units were found. Thus in two experiments of this type altogether 18 DSCT against 11 VSCT units were recorded. With the arrangement described the DSCT units were found in the lateral funiculus from the surface down to about 0.5 mm's depth whereas the VSCT units were found from this level down through the rest of the spinal cord section. However, a few DSCT units were encountered in the region where most VSCT units are found, and two VSCT units were recorded at depths of only about 60 and 100 μ respectively. It is concluded that the two spino-cerebellar tracts occupy fairly well-defined areas, but

that some DSCT axons are found within Gowers' fasciculus and some VSCT axons within Flechsig's fasciculus.

The results on mass discharge recording from the ventral and dorsal spino-cerebellar tracts suggested that the dorsal tract was almost completely uncrossed, whereas the ventral one was practically completely crossed (OSCARSSON 1956). That the dorsal tract is uncrossed was confirmed in the present investigation. Only in one case was a crossed DSCT unit encountered. This unit was recorded at a depth of about 400 μ and responded with a single spike on group Ia stimulation of the contralateral quadriceps nerve. The first spike was followed by a second one when the stimulus strength was increased to slightly supramaximal for group I. Repetitive stimulation of very low threshold group I muscle afferents in the contralateral biceps p.+semitendinosus nerve resulted in inhibition. No effects were obtained from the corresponding ipsilateral nerves. This unit was a typical DSCT unit (cf. LAPORTE et al. 1956 b, LUNDBERG and OSCARSSON 1956) except for the fact that it was crossed. Against this single crossed DSCT unit several hundreds of VSCT fibres have been found on contralateral muscle nerve stimulation, despite the fact that more DSCT than VSCT units are found on combined stimulation of ipsilateral and contralateral nerves.

B. *Antidromic stimulation*

In most experiments the spinal half (except dorsal column) was dissected at the upper thoracic region. This permitted the VSCT mass discharge to be recorded (OSCARSSON 1956) at the same times as the response in single VSCT units and made it possible to stimulate the units antidromically. In experiments with a comparatively large mass discharge all the units could be discharged antidromically on stimulation of the dissected half of the spinal cord, whereas in experiments with a small discharge often some of the VSCT units could not be excited unless a very high stimulus strength was used. In the latter cases the tract probably had been damaged during the dissection. That most or all of the assumed VSCT units actually reach the region of the superior cerebellar peduncle was shown in three experiments. After decerebration the peduncle was exposed and the VSCT mass discharge was recorded from its surface (cf. OSCARSSON 1956). Altogether 19 VSCT units were found in Gowers' fasciculus at the upper lumbar region and all of them

could be discharged antidromically on stimulation with single shocks through the electrode at the superior cerebellar peduncle.

In the previous paper it was shown that the conduction velocity of the fastest VSCT fibres amounted to about 120 m/sec. The conduction velocity assessed for single VSCT fibres from the latency of the antidromic spike confirmed this finding. Most of the units had velocities between 80 and 120 m/sec and only a few lower or higher velocities. The mean velocity was 93 m/sec (50 units).

C. *Behaviour on stimulation of muscle nerves*

The VSCT units respond with a single spike on stimulation of group I muscle afferents in contralateral nerves as could be expected from the findings on mass discharge recording (OSCARSSON 1956). In experiments with separation between the subgroups Ia and Ib (BRADLEY and ECCLES 1953, ECCLES et al. 1957 a) as judged from the dorsal root entry zone recording, it was confirmed that the VSCT neurons receive excitatory action from Ib but not from Ia afferents. Not even subliminal action was obtained from a Ia volley as tested in two experiments with a virtually complete separation between the group Ia and Ib volleys in the hamstring nerve. The stimulus to the nerve was adjusted to give a postsynaptic spike only occasionally. This "labile" spike was used for testing the effect of a preceding pure group Ia volley. 13 units were examined and none was appreciably influenced from the Ia afferents.

Whereas all VSCT units are characterized by the appearance of a single spike on group I stimulation, two types may be distinguished on stimulation supramaximal to group I. In most units further spikes do not appear with increased stimulus strength as is illustrated in Fig. 2. The contralateral hamstring nerve was stimulated and recording was simultaneously performed from the dissected spinal half (upper beam) and from a VSCT fibre within the ventro-lateral funiculus. Records 1—3 and 6 are shown for identification. The VSCT mass discharge is just appreciable in record 1 and no spike appears in the unit. When the mass discharge was increased to about one third maximal the unit was discharged as shown in record 2. In

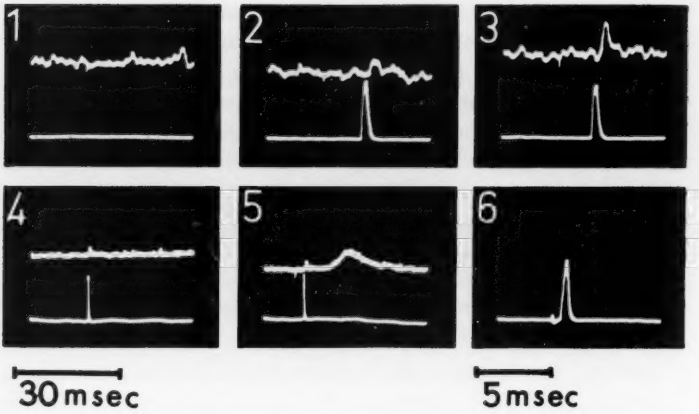


Fig. 2. VSCT unit of I-type. Simultaneous recording from left dissected spinal half (except dorsal column) and from fibre in left ventro-lateral funiculus (records 1—5). Records 1—3 obtained on a fast sweep on increasing stimulation of the right hamstring nerve. In record 1 the stimulus evokes a just appreciable VSCT mass discharge. The VSCT mass discharge is maximal in record 3. Record 4 (slower sweep) was obtained on stimulation of the right hamstring nerve with the same strength as that used in record 3. Record 5 obtained on supramaximal stimulation of the hamstring nerve. Lower amplification of mass discharge in records 4 and 5. Record 6 shows antidromic spike on stimulation of the dissected spinal half. Distance dissected spinal half—site of micro-electrode recording 6.5 cm. Nembutal anaesthesia.

record 3 the strength was increased to stimulate approximately all the group I afferents. This caused an increase in the mass discharge and a slight shortening of the latency. Record 6 shows the antidromic spike appearing on stimulation of the dissected spinal half. The stimulus strength was the same in record 4 as in record 3, but the sweep speed made slower. The amplification of the spinal half recording had been decreased and the VSCT mass discharge appears as a small hump. In record 5 the hamstring nerve was stimulated supramaximally and the VSCT discharge is followed by a large longlasting potential which is due to activity in ascending fibres which are activated from high threshold muscle nerve afferents and which do not belong

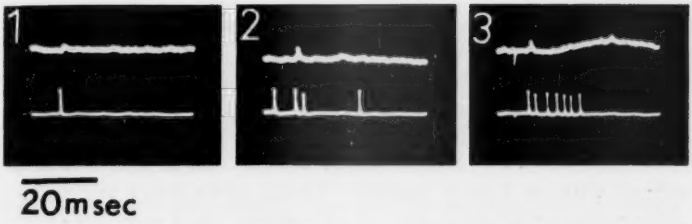


Fig. 3. VSCT unit of E-type. Simultaneous recording from left dissected spinal half (except dorsal column) and from fibre in left ventro-lateral funiculus on increasing stimulation of the right hamstring nerve. First and fourth spike in record 2 due to the spontaneous activity of the unit. Nembutal anaesthesia.

to the VSCT (cf. OSCARSSON 1956, 1957 b, c). The lower beam shows that further spikes do not appear on supramaximal stimulation.

Most of the encountered VSCT units behaved in conformity with the one shown in Fig. 2. These units will be denoted as I-units as they receive predominantly inhibitory action from high threshold muscle nerve afferents as will be shown in Chapters IV and V. The rest of the units behaved differently, in that further spikes appeared on increasing the stimulation to supramaximal for group I. These units receive predominantly excitatory action from high threshold muscle nerve afferents and will be denoted as E-units. Fig. 3 illustrates a typical E-unit. The contralateral hamstring nerve was stimulated and recording was performed simultaneously from the dissected spinal half (upper beam) and a fibre within the ventro-lateral funiculus. Already with a small VSCT mass discharge a spike appears in the unit (record 1). When the stimulus strength was increased to be slightly supramaximal to group I, as shown by the small late potential in the mass discharge recording (cf. OSCARSSON 1957 c) a second spike appears (record 2), and on supramaximal stimulation the "Ib spike" is followed by a train of impulses (record 3).

The second spike in record 2 appears with such a short latency that the excitatory action may be due to monosynaptic transmission. The later spikes appearing in record 3 also have

latencies which may accord with monosynaptic transmission if they are caused by impulses in slowly conducting group II or III afferents as seems probable. In other E-units supramaximal stimulation usually led to the appearance of 2—4 further spikes but sometimes to as many as 6—7. In some units the spikes appeared as early as in the unit shown in Fig. 3, but in others with a longer latency. In the latter cases the spikes appeared only with high stimulation strengths and were probably evoked from very high threshold afferents. It is therefore not necessary to assume polysynaptic transmission in these cases. However, for a definite conclusion about mono- or polysynapticity further experiments are needed.

The I- and E-units were found to be unequally distributed among the units monosynaptically activated from Ib afferents in the hamstring and quadriceps nerves. Of 171 encountered "hamstring units" only 17 (10 per cent) were of E-type, whereas of 38 "quadriceps units" 9 (24 per cent) were E-units.

D. *Resting behaviour*

The resting activity of the VSCT units differed characteristically from that of the DSCT units. Both kinds of units are influenced by anaesthesia and their behaviour will be described first as it appears in the anaesthetized cat and then as it appears in the not anaesthetized one.

In the anaesthetized animal most DSCT units have a resting activity of about ten impulses per second (LAPORTE and LUNDBERG 1956). Though the frequency varies from unit to unit, the activity is usually conspicuously regular. The VSCT units of I-type are very seldom spontaneously active. When spontaneous, they have low frequencies at about one per second, and the activity is irregular with the impulses often grouped in small bursts. The same irregularity characterizes the E-units which usually are spontaneous and have frequencies up to twenty or thirty per second.

In the not anaesthetized animal the resting activity of the DSCT units is as regular as in the anaesthetized one but has a higher mean frequency of about twenty per second. A record from a DSCT unit under resting conditions is shown in Fig. 4

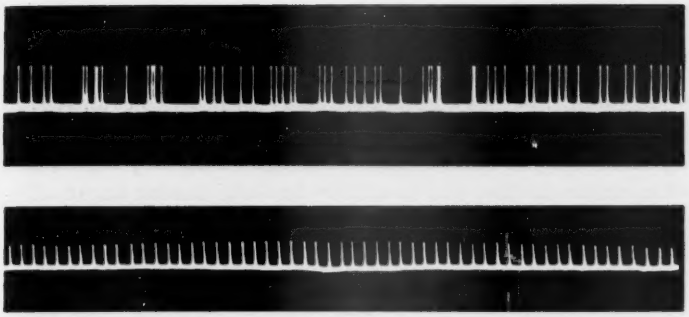


Fig. 4. Comparison of resting activity in a VSCT (upper record) and a DSCT (lower record) unit. The VSCT unit identified as being monosynaptically discharged from group I afferents in the contralateral hamstring nerve. The DSCT unit identified as being discharged from very low threshold group I afferents in the ipsilateral hamstring nerve and as responding with a double spike on stimulation including group II afferents. Unanaesthetized preparation.

(lower record). The regularity of the impulses in this case is not exceptional; units with an even more marked regularity are sometimes found. The VSCT units of I-type are often spontaneous in this type of preparation, but also silent units are encountered. The spontaneous I-units have often frequencies amounting to twenty or thirty per second and the activity is irregular as in the anaesthetized animal. The upper record in Fig. 4 shows a typical I-unit under resting conditions. The record shows the characteristic bursts of impulses described above. The E-units are very similar to the I-units, but have usually a higher frequency. Silent E-units have not been encountered in the not anaesthetized preparations.

DISCUSSION

The findings reported in the first paper in this series (Oscarsson 1956) suggested that the VSCT neurons were discharged mainly or exclusively from Golgi tendon organ afferents. In the present investigation it was shown that, when recording from

single VSCT units, the action potential regularly appeared with the Ib volley. Furthermore, neither excitatory nor inhibitory effects could be shown to converge onto VSCT neurons from the Ia volley. Recent quantitative analyses (ECCLES et al. 1957 a, LAPORTE and BESSOU 1957) have shown that the Ia volley is due to activity in muscle spindle afferents with only inconsiderable contamination due to activity in Golgi tendon organ afferents, and that the Ib volley is due to activity in Golgi tendon organ afferents with only little contamination due to activity in other afferents. Consequently, it seems now possible to conclude definitely that the VSCT neurons are activated from Golgi tendon organ afferents but not from group I muscle spindle afferents.

The VSCT mass discharge on supramaximal stimulation of contralateral muscle nerves was described as a well synchronized potential with a duration of a few milliseconds (OSCARSSON 1956). Most of the encountered VSCT units behaved as could be expected from this finding, *i. e.* a single spike with a short latency appeared on supramaximal stimulation of contralateral muscle nerves. However, in some units the "Ib spike" was followed by a train of action potentials appearing on stimulation supramaximal to group I. These units were denoted as E-units. The existence of transitional forms between these units and the more common I-units will be shown later in this paper (Chapters IV and V). Consequently it is most probable that also these units belong to the VSCT and continue to the cerebellum. Recording of the VSCT mass discharge from the superior cerebellar peduncle usually showed no discharge following the first well defined potential, the "Ib discharge". This, however, is quite explicable as the E-units only constitute 10—25 per cent of the total number of the VSCT units and as the later spikes appearing in these units are temporally dispersed. The resulting late mass discharge from the E-units will probably not amount to more than a few per cent of the total VSCT discharge due to the excitatory action from the Ib afferents, and such a small discharge is hardly appreciable against the background noise. In two (out of nine) experiments with recording from the superior cerebellar peduncle in which a large nerve (the sciatic

nerve and the L VII dorsal root respectively) was used for stimulation the base line was in fact not reached immediately after the "Ib discharge". This was followed by a small discharge forming a low plateau. One of these experiments was shown in Fig. 3 in the previous paper (OSCARSSON 1956). As shown in the figure the plateau disappeared together with the "Ib discharge" after a superficial lesion in the ventro-lateral quadrant of the spinal cord. Possibly this late discharge represented activity in VSCT units of E-type.

SUMMARY

The VSCT mass discharge was recorded simultaneously with the discharge in single VSCT fibres on stimulation of various muscle nerves in the contralateral hindlimb.

Identification of single VSCT units is described.

The VSCT neurons receive excitatory action from Golgi tendon organ afferents, but no appreciable effects from group I muscle spindle afferents.

Two types of VSCT units are distinguished. Both respond with a single spike on group I stimulation but on supramaximal stimulation some units respond with further spikes. These units have been denoted as E-units, as they receive predominantly excitatory action from high threshold muscle nerve afferents. The other type makes out about 90 per cent of the VSCT units identified from the hamstring nerve, and about 75 per cent of the units identified from the quadriceps nerve, and in these units supramaximal stimulation does not result in the appearance of further spikes. These units have been denoted as I-units.

The resting behaviour of the two types of VSCT units is described and compared with that of the DSCT neurons.

Stimulation of the VSCT at the superior cerebellar peduncle regularly evoked an antidromic spike in the VSCT units recorded at the upper lumbar region. It is concluded that most or all of the assumed VSCT units reach the superior cerebellar peduncle.

The conduction velocity of the VSCT fibres assessed from the latency of the antidromic spike usually varied between 80 and 120 m/sec. The mean velocity was 93 m/sec (50 units).

Chapter II

Characteristics of impulse transmission from Ib afferents to VSCT neurons

This chapter deals with characteristics of the transmission from Golgi tendon organ afferents to VSCT neurons. In many of the experiments simultaneous recording from the DSCT and a suitable ventral root permitted comparison with the transmission in the better known, likewise monosynaptic, connections between group I afferents and DSCT neurons (LLOYD and MCINTYRE 1950, LAPORTE et al. 1956 a, b, HOLMQVIST et al. 1956), and between group I afferents and motoneurons. It will be shown that the VSCT connection is more susceptible to asphyxia and anaesthesia than the DSCT connection. The depression of the synaptic transmission due to anaesthesia results in a large subliminal fringe which has been used for assessing the time course of the decay of the subliminal excitatory action in the VSCT neurons. The subliminal fringe has also made it possible to study the post-tetanic potentiation in the VSCT which has a steeper rising phase than the potentiation in the monosynaptic reflex. Finally the depression of the transmission from primary afferents, which follows in the wake of a discharge of the VSCT neurons, has been investigated.

In addition, VSCT neurons have been shown to receive inhibitory Ib action as well as the excitatory one.

RESULTS

A. *Susceptibility to asphyxia and anaesthesia*

The DSCT discharge was found to be very stable under varying experimental conditions as might be expected from the finding of a strong synaptic coupling between primary afferents and tract neurons (LLOYD and MCINTYRE 1950, HOLMQVIST et al.

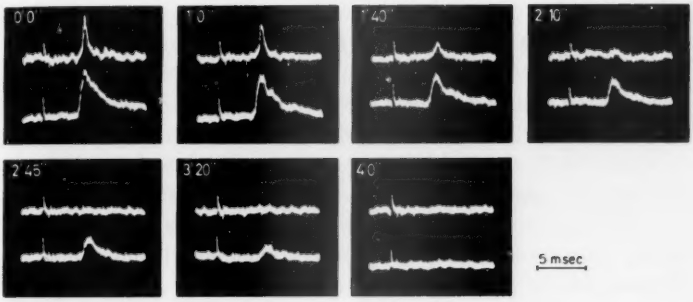


Fig. 5. Decrease of VSCT and DSCT discharges on asphyxia. Simultaneous recording of the VSCT discharge from the left dissected spinal half (except dorsal column) (upper beam) and of the DSCT discharge from the right dissected spinal half (except dorsal column) on slightly supramaximal group I stimulation of the right hamstring nerve. Upper left record obtained previous to cardiectomia in order to induce asphyxia. Other records obtained at various intervals (time given in minutes and seconds) after cardiectomia. Nembutal anaesthesia.

1956). In contrast, the VSCT discharge varied much and was influenced by slight changes in the general condition of the preparation. Sometimes the VSCT discharge diminished, or even completely disappeared, during experiments in which the DSCT discharge was hardly influenced. Probably the decrease of the discharge was due to adverse circulatory disturbancies, either local or general, leading to asphyxia of the synaptic region. That the monosynaptic connection of the VSCT is much more susceptible to asphyxia than that of the DSCT is evident from the experiment illustrated in Fig. 5. The hamstring nerve was stimulated supramaximally and the VSCT discharge recorded from the contralateral dissected spinal half (upper beam) and the DSCT discharge from the ipsilateral half (cf. LAPORTE et al. 1956 a, OSCARSSON 1956). The upper left record shows the initial discharges. In order to induce asphyxia abruptly the cat was cardiectomized. The effect on the DSCT and VSCT discharges was followed and some of the obtained records are shown in the figure. After about 2.5 minutes the VSCT discharge had completely disappeared whereas the DSCT discharge was

abolished only after 4 minutes. In another experiment, after 1 minute, the VSCT discharge had decreased to less than half of its original value whereas the DSCT discharge was only little reduced. In this experiment the VSCT discharge was abolished after 2—2.5 and the DSCT discharge after about 4 minutes.

The VSCT discharge was also much more susceptible to anaesthesia than the DSCT one. The VSCT discharge appearing on stimulation of single muscle nerves, such as the semitendinosus or biceps nerves, was always very small and often not appreciable in the anaesthetized cat. In the not anaesthetized animal similar stimulation usually evoked fairly large potentials. No marked difference was found between the DSCT discharge evoked in the anaesthetized and the not anaesthetized cat.

B. *Decay of subliminal excitatory Ib action. Inhibitory Ib action*

In the anaesthetized animal stimulation of a single muscle nerve evoked a small or not appreciable mass discharge. However, a large VSCT discharge could be obtained on combined stimulation of several nerves. This shows that stimulation of a single muscle nerve leaves a large subliminal fringe which may be discharged on stimulation of other muscle nerves, and indicates convergence of Ib afferents in different nerves onto the same VSCT neurons.

The time course of the decay of the subliminal excitation was assessed in some experiments. If the connection is exclusively monosynaptic this time course may be considered as the time course of the excitatory post-synaptic potential (cf. ECCLES 1946, LLOYD 1946, COOMBS, ECCLES, and FATT 1955, COOMBS, CURTIS, and ECCLES 1956). In the experiment illustrated in Fig. 6: A, the VSCT discharge evoked from the semimembranosus nerve was small and the discharge from the biceps p.+semitendinosus nerve fairly large. The effects of conditioning with a slightly submaximal group I stimulus to the semimembranosus nerve on the VSCT discharge evoked by supramaximal group I stimulation of the biceps p.+semitendinosus nerve were plotted to give the curve in the figure. The ordinate shows the amplitude of the VSCT discharge in per cent of the amplitude of the unconditioned discharge and the abscissa the time interval between

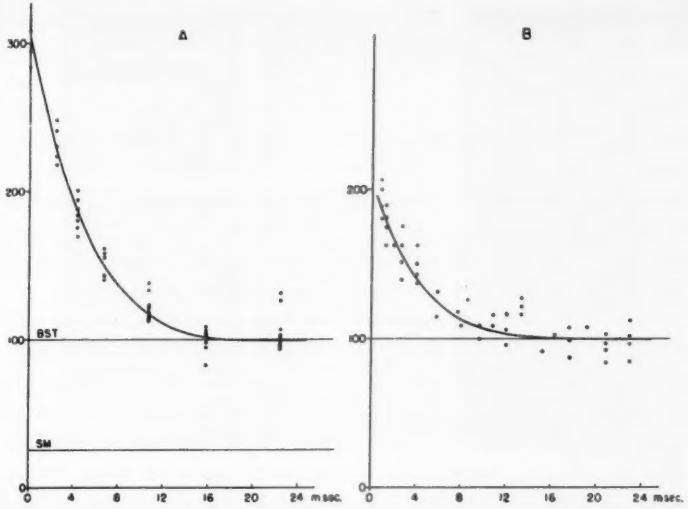


Fig. 6. The time course of the decay of the subliminal excitatory action. Abscissa: interval between conditioning and testing primary afferent volleys. Ordinate: amplitude of conditioned VSCT mass discharge in per cent of amplitude of unconditioned one. *A.* Conditioning with slightly submaximal group I stimuli to the semimembranosus nerve (SM) and testing with slightly supramaximal group I stimuli to the biceps p.+semitendinosus nerve (BST). Amplitude of VSCT mass discharge evoked by the conditioning volley shown as thin line marked SM. *B.* Conditioning with slightly submaximal group I stimuli to the hamstring nerve and testing with slightly supramaximal group I stimuli to the same nerve. Nembutal anaesthesia.

the conditioning and testing volleys. The facilitation is maximal at zero interval and decreases with increasing interval along an approximately exponential curve. No facilitation is detectable at intervals longer than about 15 msec. To obtain a correct value of the activation of the subliminal fringe at zero interval, the amplitude of the discharge should be reduced with that part which is due to VSCT fibres activated solely from the semimembranosus nerve. The discharge evoked from this nerve was, however, small, and the contribution on simultaneous stimulation of both nerves was probably even smaller due to occlusion between the two volleys. The curve may consequently be regarded as a

representation of the decay of the subliminal excitation only slightly distorted at zero interval.

The curve in Fig. 6: B was obtained on conditioning and testing with the same nerve, the hamstring nerve. Obviously the curve is very similar to that in Fig. 6: A. With decreasing interval the discharge increases until the testing stimulus is delivered so near the conditioning one as to fall within the refractory period of the afferent fibres. This curve furthermore suggests that there is little depression of the transmission to the VSCT neurons in the wake of a preceding discharge.

The time course of the decay of the subliminal excitatory Ib action could also be appreciated when recording from single VSCT fibres. The "labile" spike evoked on weak stimulation from one muscle nerve was often facilitated on stimulation of other muscle nerves. In experiments with separation between the Ia and Ib volleys this facilitation appeared with the Ib volley. The facilitation was maximal when the testing and conditioning volleys were approximately simultaneous and could usually be displayed at intervals up to 10 or 15 msec. In a few cases it was demonstrable up to 20 msec.

By the use of a labile spike for testing, convergence of inhibitory group I action could be displayed in some cases. Such inhibitory action was observed in the VSCT unit shown in Fig. 7. Records 1—3 are shown for identification. In record 1 the hamstring nerve is stimulated with a strength about maximal for group I. This results in a single spike about half a msec previous to the mass discharge. Record 2 shows the antidromic spike on stimulation of the dissected half of the spinal cord. Record 3, obtained with a slower sweep speed than record 1, shows that also supramaximal stimulation of the hamstring nerve evokes only a single spike in the unit. This classifies the unit as an I-unit (Chapter I). In record 4 the stimulus strength was adjusted to give a mass discharge about half maximal. With this strength the spike still appeared regularly. The stimulation was unchanged when record 5 was obtained but preceded by a stimulus to the quadriceps nerve. The stimulus to the latter was of such strength as to evoke an ingoing volley of about half the magnitude of a maximal group I volley.

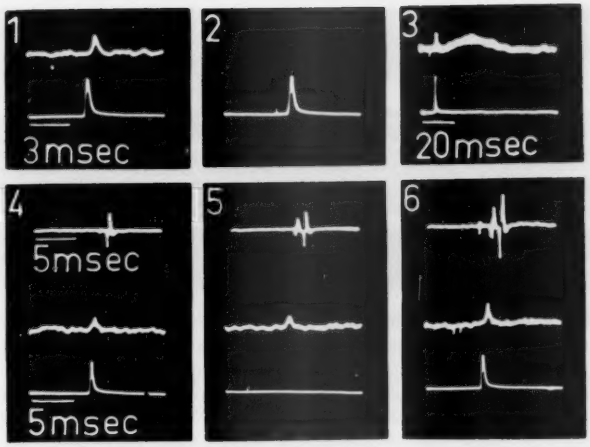


Fig. 7. Inhibitory action from group I afferents converging onto VSCT neuron. Simultaneous recording (records 1 and 3) from left dissected spinal half (except dorsal column) and from VSCT fibre in left ventro-lateral funiculus (lower beam). Simultaneous recording (records 4—6) from right L VII dorsal root entry zone (upper beam), left dissected spinal half (middle beam), and the VSCT fibre (lower beam). Records 1 and 2 on a fast sweep to show the latency of the orthodromic spike obtained on slightly supramaximal group I stimulation of the right hamstring nerve and the latency of the antidromic spike obtained on stimulation of the dissected spinal half. Record 3, with a slow sweep, obtained on supramaximal stimulation of the right hamstring nerve. Stimulus strength to the hamstring nerve adjusted to evoke about half a maximal group I volley in records 4 and 5. Stimulus to the hamstring nerve preceded by stimulation of the right quadriceps nerve in record 5. Stimulus strength to the latter evoking about half a maximal group I volley. Record 6 obtained on slightly supramaximal group I stimulation of the quadriceps and hamstring nerves. Nembutal anaesthesia.

Conditioning with this volley caused inhibition of the spike, thus displaying group I inhibitory action to a VSCT neuron. In record 6 both the conditioning and testing stimuli were increased to maximal for group I. Under these circumstances the inhibitory action from the quadriceps nerve is not strong enough to inhibit the spike evoked from the hamstring nerve.

When group I inhibition was found in preparations with Ia

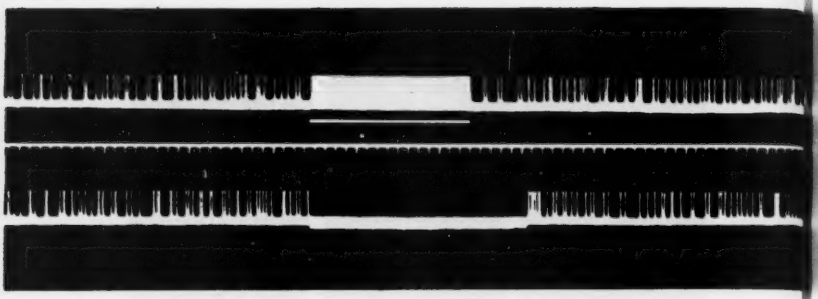


Fig. 8. Excitatory and inhibitory Ib effects on repetitive stimulation. Recording from a VSCT unit of I-type which was discharged on group I stimulation of the contralateral hamstring nerve and inhibited on group I stimulation of the contralateral quadriceps nerve. Repetitive stimulation of the hamstring (upper record) and quadriceps (lower record) nerve at a frequency of about 200 per second. Duration of the stimulation indicated by a white line in the upper record and as a broadening of the base line (shock artefacts) in the lower record. 100 msec time intervals. Slight nembutal anaesthesia.

and Ib separation it appeared with the Ib volley. In other experiments the inhibition was shown to appear simultaneously with the VSCT mass discharge in the tract. This suggests that the inhibition, as the monosynaptic excitation, is exclusively due to Ib afferents. The inhibition could often be demonstrated when the ingoing volleys were about simultaneous, but sometimes it was necessary to evoke the conditioning volley about half a msec previous to the testing one. The inhibitory action was sometimes detectable at intervals up to about 10 msec but often only at intervals up to a few msec.

The short duration of the excitatory and inhibitory Ib effects is well displayed on tetanic stimulation. In Fig. 8 a VSCT unit is shown which was discharged from the hamstring nerve and inhibited from the quadriceps nerve. Tetanic stimulation of the hamstring nerve at a rate of about 200 per second resulted in a discharge which well followed the applied frequency (upper record). Cessation of the stimulation resulted in a slight depression followed by a return to the previous resting activity after some msec. Similarly tetanic stimulation of group I

afferents in the quadriceps nerve caused an abrupt inhibition of the resting activity (lower record). At the end of the tetanic stimulation there was a slight rebound followed by a reappearance of the resting activity.

C. *Effect of antidromic stimulation and ability to follow high repetition rates*

In the previous section some evidence was given that the transmission from Ib afferents to VSCT neurons is little depressed after discharge of the tract neurons. The mass discharge evoked by a testing volley was not appreciably reduced on decreasing the interval between the conditioning and testing volleys of the same nerve as long as the interval was longer than the refractory period of the primary afferents. Findings on single units substantiate this observation. The effect of antidromic stimulation was judged by the response of a subsequent orthodromic stimulation. If the unconditioned orthodromic stimulation was made successively weaker a point was reached at which the stimulus evoked a post-synaptic spike just each time. A further reduction of the stimulus strength resulted in a "labile" spike appearing only occasionally and then in the complete disappearance of the spike response. The margin between the stimulus causing a "just constant spike" and a stimulus not evoking any post-synaptic discharge was usually narrow.

In no unit was the spike evoked by strong orthodromic stimulation suppressed when preceded by a conditioning antidromic stimulation. However, when the stimulus was adjusted to give a "just constant spike", depression usually could be demonstrated, but in some cases the depression was as weak as to necessitate testing with a labile spike. Fig. 9 A and B shows representative curves obtained from two VSCT units. The depression was in both cases judged by the effect on a just constant orthodromic test spike, and the plottings were obtained as per cent of responses of total tests. Thus, the first plotting in 9: A was obtained from 22 tests of which no one caused a post-synaptic spike and the second plotting from 21 tests of which

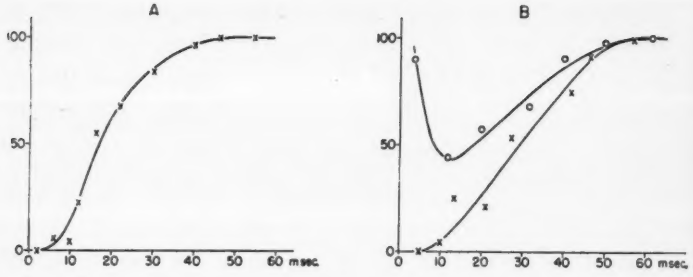


Fig. 9. Time course of depression of orthodromic transmission after discharge of VSCT units. Abscissa: interval between conditioning and testing stimuli. Ordinate: depression of orthodromic response in per cent of unconditioned value (see text). Two units (A and B), both discharged from the hamstring nerve, are shown. Plottings shown as crosses obtained on antidromic conditioning and plottings shown as circuits on homosynaptic conditioning with a slightly submaximal group I stimulus. Nembutal anaesthesia.

2 succeeded in discharging the VSCT unit. In the different units the depression lasted between 45 and 80 msec (10 units).

The effect of a conditioning homosynaptic volley was also tested. Sometimes no depression was found as was the case for the unit shown in 9: A, but in others a depression of similar type as that obtained on antidromic conditioning resulted. In some units the depression was smaller and delayed as was the case for the unit shown in 9:B (circuits). The weaker depression on orthodromic conditioning is probably partly due to a survival of excitatory action from the conditioning volley.

The weak depression which follows activity in the VSCT units permits transmission at high impulse frequencies. Most of the units actually follow frequencies up to several hundreds per second and sometimes frequencies as high as 600. The ability to follow these repetition rates was not appreciably reduced for stimulation periods as long as seconds. The highest frequency transmitted was 650 which was found for a unit activated from the hamstring nerve.

During the course of experiments also DSCT units were tested. As far as could be judged from the 10 units examined, the depression was practically identical in strength and duration

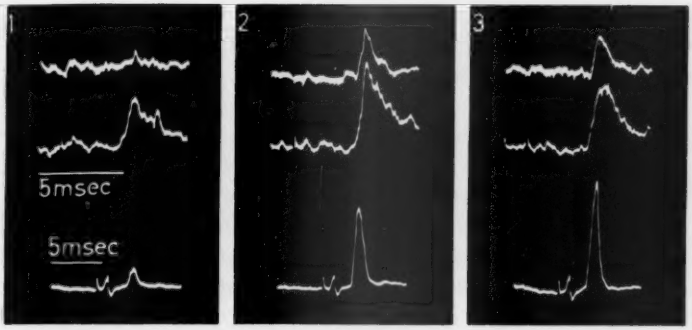


Fig. 10. Post-tetanic potentiation in VSCT, DSCT, and monosynaptic reflex. Simultaneous recording from left dissected spinal half (except dorsal column) to show the VSCT discharge (upper beam), right dissected spinal half (except dorsal column) to show the DSCT discharge (middle beam), and right L VII ventral root to show the monosynaptic reflex (lower beam) on slightly supramaximal group I stimulation of the right biceps p.+semitendinosus nerve. Record 1 obtained before and records 2 and 3, 13.5 and 40.5 seconds after one minute's tetanization at a frequency of 250 stimuli per second. Nembutal anaesthesia.

with that found in the VSCT units. The DSCT units are known to follow high stimulation frequencies (HOLMQVIST et al. 1956).

D. *Post-tetanic potentiation*

The existence of a large subliminal fringe in the anaesthetized animal was also displayed by the effect of tetanic stimulation. A marked post-tetanic potentiation of the VSCT discharge was regularly observed in experiments on anaesthetized cats. A series of experiments were performed in order to compare the post-tetanic potentiation in the two spino-cerebellar tracts and in the monosynaptic reflex. In most experiments tetanic stimulation with slightly submaximal group I stimuli during one minute and at a frequency of 250 per second was used. This causes an almost maximal potentiation of the monosynaptic reflex (LLOYD 1949). The potentiation was tested with single shocks delivered at intervals of 2.7 seconds. Recording was performed simultaneously from the DSCT, the VSCT, and a suitable ventral root. Records from such an experiment are shown in Fig. 10. The left

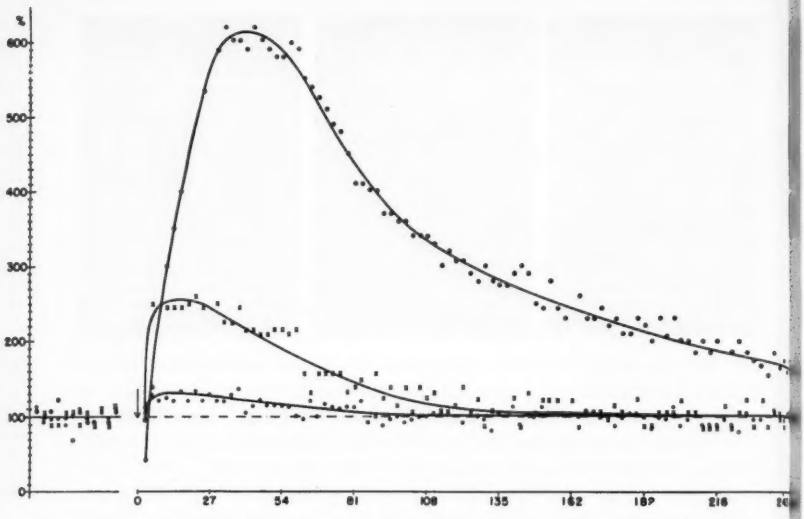


Fig. 11. Comparison of post-tetanic potentiation in DSCT (dots), VSCT (crosses), and monosynaptic reflex (circuits). Plottings obtained from recording as in Fig. 10. Abscissa: time in seconds. Ordinate: amplitude of mass discharges in per cent of value obtained previous to tetanization. Arrow marks end of one minute's tetanization of the biceps p.+semitendinosus nerve at a frequency of 250 stimuli per second. The effect of tetanization was tested with slightly supramaximal group I stimuli to the biceps p.+semitendinosus nerve at intervals of 2.7 sec. Nembutal anaesthesia.

record was obtained before, middle 13.5, and right 40.5 seconds after tetanization of the biceps p.+semitendinosus nerve. Previous to the tetanic stimulation the VSCT discharge (upper beam) is just appreciable above the noise level but increases considerably after. The potentiation of the DSCT discharge (middle beam) is of smaller magnitude. The potentiation in the two tracts was about maximal when record 2 was obtained and has already declined in record 3. The monosynaptic reflex was potentiated to a higher degree than the VSCT discharge and reached a maximum after about 40 seconds when record 3 was obtained.

The potentiation in the spino-cerebellar tracts was unusually

large in the experiment illustrated in Fig. 10. More often the potentiation was of the magnitude shown in Fig. 11. This figure also displays the difference in time course which was regularly found between the potentiation in the two spino-cerebellar tracts and the monosynaptic reflex. The discharges of the tracts always increased rapidly to reach an early maximum after about 15 seconds, whereas the monosynaptic reflex increased more slowly and became maximal after about 40 seconds. The steepness of the rising phase and also the duration of the potentiation depends on the duration of the tetanic stimulation, as shown *e. g.* for the transmission in sympathetic ganglia (LARRABEE and BRONK 1947), for the monosynaptic reflex (LLOYD 1949), and for the neuro-muscular transmission (LILEY and NORTH 1953). It was consequently of interest to test the effect of short tetanic stimulation on the potentiation in the spino-cerebellar tracts. The difference in time course between the potentiation of the monosynaptic reflex and the discharges in the two tracts was found also after short tetanizations. Following a tetanus of only five seconds' duration the monosynaptic reflex became maximal after about 12 seconds, whereas the tract discharges became maximal already after about 6 seconds.

The increase of the VSCT discharge following tetanic stimulation of one minute's duration (six experiments) was between 55 and 420 per cent whereas the increase of the DSCT discharge was between 20 and 50 per cent. The potentiation of the monosynaptic reflex was always greater than that of the VSCT discharge.

The post-tetanic potentiation is known to be a pre-synaptic phenomenon (cf. for example LARRABEE and BRONK 1947, LLOYD 1949, ECCLES and RALL 1951) and hence evoked only on homosynaptic conditioning. This was easily displayed also in the present experiments. Fig. 12 shows the effect of heterosynaptic conditioning with tetanic stimulation of the biceps p.+ semitendinosus nerve on the test discharge evoked from the semimembranosus nerve. During the tetanus the VSCT test discharge (lower beam) is increased indicating excitatory convergence of afferents from the two nerves onto the same VSCT

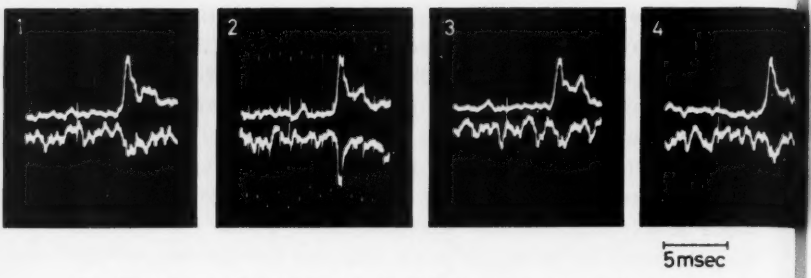


Fig. 12. Absence of post-tetanic potentiation on heterosynaptic conditioning. Simultaneous recording of the VSCT discharge (lower beam) from right dissected spinal half (except dorsal column) and of the DSCT discharge from left dissected spinal half (except dorsal column) on a slightly supramaximal group I stimulation of left semimembranosus nerve. Record 1 obtained before, 2 during, 3, 2 seconds after, and 4, 15.5 seconds after one minute's tetanic stimulation of left biceps p.+semitendinosus nerve. Nembutal anaesthesia.

neurons. The DSCT test discharge is not appreciably influenced which is in accordance with the finding of HOLMQVIST et al. (1956) that convergence onto DSCT neurons is mainly limited to afferents in nerves from synergist muscles. The test discharges were not appreciably influenced by the tetanization as illustrated in records 3 and 4 obtained 2 and 15.5 seconds after the end of the tetanus. As a control the experiment was repeated with homosynaptic tetanization. This resulted in a large potentiation of the VSCT discharge and a small potentiation of the DSCT discharge.

DISCUSSION

It was shown in the first section that the VSCT discharge is more susceptible to asphyxia and anaesthesia than the DSCT discharge. This is not necessarily due to different properties of the two types of tract neurons, since the monosynaptic coupling of the DSCT is characterized by an "extremely powerful synaptic articulation" (LLOYD and MCINTYRE 1950, HOLMQVIST et al. 1956) which has been correlated to unique histological features (SZENTAGOTHAI and ALBERT 1955). The susceptibility

of the VSCT discharge probably explains why the first potential recorded from the cerebellar surface previously has been considered to be due solely to the DSCT (GRUNDFEST and CAMPBELL 1942, MCINTYRE 1951, LAPORTE et al. 1956 a). This conclusion was based on the finding that this potential, at least in some experiments, disappeared after section of the ipsilateral Flechsig's fasciculus. Recently, the first potential has been shown to be due to both the spino-cerebellar tracts and consequently not abolished by ipsilateral section of the DSCT (OSCARSSON 1956). In the previous experiments the VSCT discharge was probably depressed due to anaesthesia or slight circulatory disturbancies not markedly affecting the DSCT discharge.

The existence of a large subliminal fringe in the VSCT in the anaesthetized cats made it possible to assess the time course of the decay of the subliminal excitatory action (cf. LLOYD 1946). This was represented by a smooth, approximately exponential curve. The smoothness of the curve indicates that the excitatory action is due to a unitary process; presumably the curve represents the decay of the excitatory post-synaptic potential. It also suggests that the connection between group I afferents and VSCT neurons is exclusively monosynaptic. The time course obtained from the curves is similar to that assessed for the excitatory post-synaptic potential of the motoneurons (ECCLES 1946, LLOYD 1946, COOMBS et al. 1955, COOMBS et al. 1956). As yet no data are available concerning the post-synaptic potentials evoked in the DSCT neurons.

Inhibitory Ib action was sometimes found to converge onto VSCT neurons. It appeared with a very short latency, but in conformity with the findings on motoneurons (ECCLES, FATT, and LANDGREN 1956, ECCLES 1957) and DSCT neurons (CURTIS, ECCLES, and LUNDBERG, personal communication), the inhibition might be expected to be mediated by interneurons. The inhibitory action could often be displayed at intervals up to about 10 msec between the conditioning and testing volleys. Probably the decay of the Ib inhibitory action has a time course similar to that found for the excitatory action. In this respect the VSCT neurons seem to be similar to the motoneurons in which excitatory and inhibitory post-synaptic potentials decay along similar, though

not identical, time courses (LLOYD 1946, BRADLEY, EASTON, and ECCLES 1953, COOMBS et al. 1956).

Antidromic stimulation of the VSCT neurons resulted in a depression of the transmission from primary afferents to tract neurons. The depression had a time course which was approximately similar to that obtained for the motoneurons (BROOKS, DOWNMAN, and ECCLES 1950, LLOYD 1951). The depression of the VSCT neurons was slight and did not prevent them from following high impulse frequencies in the primary afferents. In contrast the motoneurons only follow low frequencies (ADRIAN and BRONK 1929, HUNT 1952). It has been suggested that, in the motoneurons, a limiting factor for the transmission at high frequencies is the post-activity hyperpolarization (ECCLES 1953, ECCLES et al. 1957 b). Another factor which may be of importance is the inhibitory Renshaw feedback (HOLMGREN and MERTON 1954, GRANIT, PASCOE, and STEG 1957). The weak depression which is found in the VSCT neurons may possibly be due to a post-activity hyperpolarization. Any inhibitory feedback mechanism similar to that found for the motoneurons is not likely to exist as it was found, in the present investigation, that the depression was an all-or-none phenomenon which at liminal stimulation of the dissected spinal half only appeared when the neuron actually was discharged antidromically.

The DSCT neurons are very similar to the VSCT neurons as regard to depression and ability to follow high impulse frequencies. The DSCT neurons are known to have a very strong synaptic coupling (LLOYD and MCINTYRE 1950, HOLMQVIST et al. 1956) and it seems not unreasonable to ascribe their ability to follow high frequencies to this fact. It is possible that the corresponding findings about the VSCT neurons may be similarly explained though probably the synaptic coupling to these neurons is weaker as suggested by the greater susceptibility to asphyxia and anaesthesia and the findings on adequate stimulation of muscle receptors (see Chapter V).

The last section dealt with post-tetanic potentiation. Comparison was made between the post-tetanic potentiation in the VSCT, the DSCT, and the monosynaptic reflex. As already noticed by MCINTYRE (1953) and HOLMQVIST et al. (1956) the

potentiation is small in the DSCT. This is to be expected as the synaptic coupling is very strong. The post-tetanic potentiation was often considerable in the VSCT though not as large as in the monosynaptic reflex. This, however, does not indicate that the subliminal fringe in the VSCT, under normal circumstances, is comparable with that of the motoneurons. In the not anaesthetized animal the post-tetanic potentiation is very small, often hardly appreciable, not only in the DSCT but also in the VSCT, whereas the potentiation of the monosynaptic reflex is great also in this type of preparation (cf. for example JEFFERSON and BENSON 1953).

The rising phase of the post-tetanic potentiation in the spinocerebellar tracts was much steeper than that in the monosynaptic reflex. The difference in steepness was especially marked after long tetanizations. The delay of the potentiation is probably caused by a depletion of the transmittor substance (cf. LILEY and NORTH 1953). Probably the depletion in the terminals supplying the tract neurons does not influence the transmission as much as the depletion in the terminals supplying the motoneurons. This may be of functional importance since it permits transmission at high frequencies for long periods of time, which has been established in both DSCT and VSCT.

SUMMARY

The transmission of nerve impulses from Golgi tendon organ afferents to VSCT neurons was studied. In some experiments simultaneous recording from the VSCT, the DSCT, and a suitable ventral root permitted comparison with the likewise monosynaptic transmission from group I afferents to DSCT neurons and motoneurons. In addition VSCT neurons were shown sometimes to receive inhibitory action from Golgi tendon organ afferents.

The transmission from Ib afferents to VSCT neurons is more susceptible to asphyxia and anaesthesia than the transmission from group I afferents to DSCT neurons.

The subliminal excitatory action in the VSCT neurons decays

smoothly along an approximately exponential curve with a time constant of about 5 msec.

VSCT neurons sometimes receive inhibitory Ib action. The inhibitory action could sometimes be displayed when the conditioning and testing volleys were approximately simultaneous, but in other cases the conditioning volley had to be evoked about half a msec previous to the testing one. The inhibitory effect was often detectable at intervals up to about 10 msec.

Antidromic stimulation of the tract neurons is followed by a weak depression of the transmission from the primary afferents with a duration of 45—80 msec. This depression does not prevent the VSCT units from following impulse frequencies in the primary afferents up to several hundreds per second.

In the anaesthetized preparation the post-tetanic potentiation in the VSCT is much larger than that in the DSCT but smaller than the potentiation in the monosynaptic reflex. In the not anaesthetized animal the potentiation is small in both the spinocerebellar tracts. The rising phase of the potentiation is steeper in the two tracts than in the monosynaptic reflex.

Chapter III

Pattern of convergence of excitatory and inhibitory Ib effects onto VSCT neurons

VSCT neurons receive excitatory as well as inhibitory action from Golgi tendon organ afferents (OSCARSSON 1956, Chapters I and II). This chapter is concerned with the pattern of convergence of these afferents onto the VSCT neurons. It will be shown that this pattern is different from that found in the DSCT and in the monosynaptic innervation of motoneurons. Excitatory convergence is extensive and not arranged according to the different functions of the muscles whereas inhibitory action is found only occasionally.

RESULTS

Convergence of Ib afferents from different dorsal roots onto VSCT neurons is indicated from experiments as that illustrated in Fig. 13. The upper beam shows the mass discharge recorded from the left dissected spinal half (except dorsal column) on stimulation of dorsal roots of the right side. The initial part of the discharge is due to activity in the VSCT (cf. OSCARSSON 1956). Record 1 was obtained on supramaximal stimulation of the S I dorsal root, and record 2 on supramaximal stimulation of the L VII dorsal root. The last record was obtained on combined stimulation of the roots. The mass discharge in this record is smaller than the sum of the discharges on stimulation of each root separately. This could be due either to occlusion of excitatory Ib actions or to inhibition. As Ib inhibition is rather uncommon (see below) and inhibition from other afferents than Ib afferents only appears after a delay of some milliseconds (Chapter IV) it is concluded that the obtained effect is due to the first possibility, *i. e.* occlusion. For comparison, the

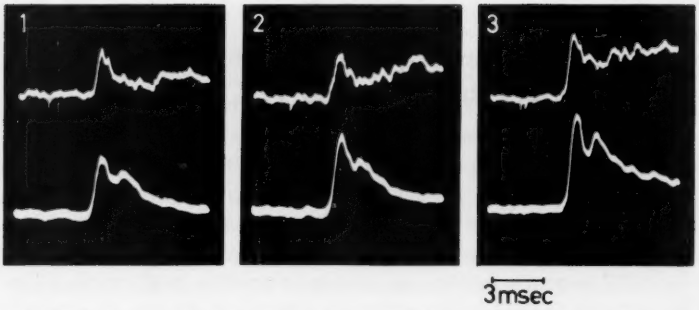


Fig. 13. Convergence of Ib afferents onto VSCT neurons shown as occlusion. Simultaneous recording from left dissected spinal half (except dorsal column) to show VSCT mass discharge (upper beam) and from right dissected half (except dorsal column) to show discharge in Flechsig's fasciculus on supramaximal stimulation of right S I dorsal root (record 1), right L VII dorsal root (record 2), and on combined supramaximal stimulation of the two roots (record 3). Higher amplification for the VSCT discharge. Nembutal anaesthesia.

mass discharge in the ipsilateral (right) dissected spinal half (lower beam) was simultaneously recorded. The initial part of the discharge is due to activity in fibres localized to Flechsig's fasciculus (LAPORTE et al. 1956 a). It appears from record 3 that there is a marked occlusion, which is in accordance with the findings of LAPORTE et al.

The subliminal fringe in the VSCT made it possible to demonstrate convergence as spatial facilitation. In the anaesthetized cat stimulation of a small muscle nerve causes a very small or not appreciable mass discharge in the VSCT, whereas stimulation of a large nerve or combined stimulation of several nerves may cause a large discharge. Record 1 in Fig. 14 was obtained on stimulation of the biceps p.+semitendinosus (BST) nerve and record 2 on stimulation of the semimembranosus (SM) nerve. A very small discharge was evoked by the BST and no appreciable one by the SM nerve. Stimulation of both nerves, however, resulted in the large discharge shown in record 3. Such a facilitation was regularly found between the hamstring nerves (the BST, SM, and anterior biceps nerves). A somewhat

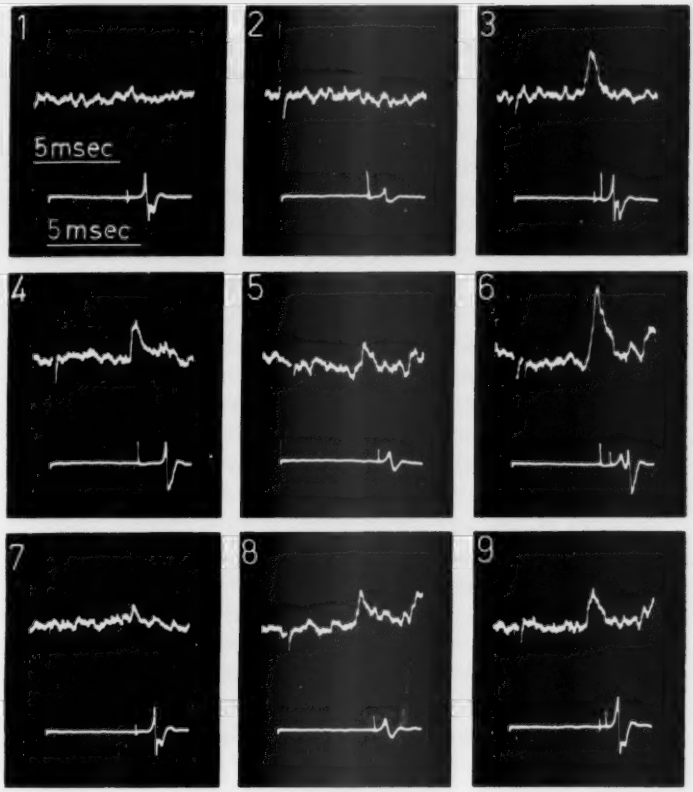


Fig. 14. Convergence of Ib afferents onto VSCT neurons shown as spatial facilitation. Simultaneous recording from left dissected spinal half (except dorsal column) to show VSCT mass discharge (upper beam) and triphasically from right L VII dorsal root entry zone. Right records show the effect of combined stimulation of the two muscle nerves which were stimulated in isolation in corresponding left and middle records. Stimulation of right biceps p.+semitendinosus nerve in records 1 and 7, right semimembranosus nerve in record 2, right triceps nerve in record 4, and right quadriceps nerve in records 5 and 8. Stimulation supramaximal to group I in all records. Nembutal anaesthesia.

less marked facilitation was observed between the hamstring nerves and the triceps nerve. In contrast there was never any appreciable facilitation between the hamstring nerves and the quadriceps nerve. In record 7 the BST nerve was stimulated and in record 8 the quadriceps nerve. The last record was obtained on combined stimulation of the two nerves and the result is simply an addition of the discharges. The discharge evoked from the quadriceps nerve was, however, often slightly facilitated by a volley in the triceps nerve as is illustrated in records 4—6. It is concluded that some VSCT neurons receive excitatory Ib action from both the hamstring nerves and the triceps nerve, and other neurons from both the quadriceps nerve and the triceps nerve.

Whereas it was easy to show facilitation on mass discharge recording, experiments to display inhibitory action from Ib afferents only yielded negative or ambiguous results also when repetitive group I stimulation was used. In a few cases repetitive stimulation of the quadriceps nerve with a stimulus slightly submaximal for group I resulted in a slight decrease of the mass discharge evoked from the hamstring nerve. The overlapping of the electrical thresholds of the group Ib and II afferents made it impossible to decide if the inhibitory effect was due only to a contamination of group II fibres or to a combined effect from Ib and II.

Though some information concerning the convergence of Ib effects onto neurons in the VSCT may be obtained from mass discharge recording, detailed information about the pattern of convergence can only be gained from recording of single units.

In the anaesthetized animal some VSCT neurons could be discharged on stimulation of one muscle nerve and sometimes even from more than one, but more often simultaneous stimulation of several nerves was needed. Convergence of subliminal excitatory action from various muscle nerves was found to be very extensive. VSCT units were identified and the stimulus to the muscle nerve (or nerves) which discharged the neuron was adjusted to give a postsynaptic spike only occasionally. This "labile" spike was used for testing convergence from other nerves. These were stimulated with a slightly submaximal

shock for group I afferents as judged from the dorsal root entry zone recording. With this method convergence of excitatory and sometimes also inhibitory Ib action onto single VSCT neurons could be demonstrated. The finding (Chapter IV) that excitatory and inhibitory actions from high threshold muscle nerve afferents converge onto VSCT neurons made some caution necessary when judging the Ib convergence. A very good help was the fact that the Ib effects have a time course different from the effects due to high threshold afferents (Chapters II and IV). Whereas the latter effects appear after a delay of some milliseconds and have a duration of tens of milliseconds, the Ib action appears when the testing and conditioning volleys are approximately simultaneous and can usually not be displayed at intervals greater than ten to fifteen milliseconds. The time course was always used as an additional criterion to low thresholdness when judging the convergence of Ib action.

The convergence of Ib effects onto single VSCT neurons was tested in a series of experiments. Only the results of the later experiments, when the technique of examination had been improved and effects from high threshold afferents were excluded with certainty, will be discussed. In 6 experiments the contralateral biceps p.+semitendinosus (BST), biceps a.+semimembranosus (BSM), triceps (T) and quadriceps (Q) nerves were prepared for stimulation. In five further experiments 9—11 contralateral muscle nerves were prepared and are listed in Table 3.

Units discharged from one of the hamstring nerves almost always received excitatory action also from the other components of this nerve. This was the case with 52 units out of 54. The excitatory action was often of about the same strength from each of the hamstring nerves and the results hardly justify a further subdivision of these units into such activated mainly from one of the nerves. Table 1 summarizes the results about the convergence onto the 52 units activated from the hamstring nerve. Excitatory convergence from the quadriceps nerve was found in not less than 14 units. 18 received inhibitory action and the rest of the units were not appreciably influenced. Convergence from the triceps nerve was usually

TABLE 1

Convergence of excitatory and inhibitory Ib actions from the quadriceps (Q) and gastrocnemius-soleus (GS) nerves onto VSCT neurons discharged from Ib afferents in the hamstring nerve

	Q	GS
Excitatory action	14	39
Inhibitory action	18	6
No effect	20	7
Number of units tested	52	52

excitatory and the effects were often quite strong. Only 6 units received inhibition and 7 were not influenced.

VSCT units discharged from the quadriceps nerve were often not influenced from the BST or BSM nerves as shown in Table 2. In some cases excitatory convergence was observed

TABLE 2

Convergence of excitatory and inhibitory Ib actions from the biceps p.+semitendinosus (BST), biceps a.+semimembranosus (BSM), and gastrocnemius-soleus (GS) nerves onto VSCT neurons discharged from Ib afferents in the quadriceps nerve

	BST	BSM	GS
Excitatory action	5	5	8
Inhibitory action	1	0	0
No effect	10	8	2
Number of units tested	16	13	10

but inhibitory action in only one unit. The convergence from the triceps nerve displayed a different pattern as 8 units out of 10 received excitatory action from this nerve.

Table 3 summarizes the results from the experiments with a greater number of contralateral muscle nerves prepared for sti-

TABLE 3

Convergence of excitatory and inhibitory Ib actions onto VSCT neurons

Exp.	Nr	Discharged by	BST	SM	BA	Q	S	GR	GS	G	P	TA	FLD
I	1	BST	++++	+++	+	+++	0	0	0	0	0	0	
	2	BST	++++	++	+	0	0	++	0	0	0	0	
	3	BST + SM	+++	+++	++	0	0	+	++	++	0	0	
	4	BST + SM	+++	+++	++	−	0	+	+	+	0	0	
	5	BST + SM	+++	+++	++	−	0	+	+	+	++	0	
	6	BST + SM	+++	+++	++	0	0	0	0	0	0	0	
	7	Q	0	0	0	++++	0	0	0	0	0	0	
	8	Q	0	0	0	++++	+	0	0	0	0	0	
	9	Q	++	0	++	++++	0	0	++	++	0	0	
II	10	BST	++++	++	++	++	0	+	+	0	0	0	
III	11	BST	++++	++	++	++	0	+	+	+	−	0	0
	12	BST + SM + GS ..	+++	+++	+	−	0	++	+++	+	+	0	0
	13	BST + Q + GS	+++	++	++	+++	+	+	+++	++	+++	0	++
IV	14	BST + BA + GS ..	+++	++	+++	0	0	0	+++	++	++	0	
	15	BST + BA + GS ..	+++	++	+++	−	0	+	+++	++	+	0	
	16	BST + BA + GS ..	+++	+	+++	−	0		+++	+	0	0	
	17	BST + BA + GS ..	+++	++	+++	0	0		+++	++	++	0	
	18	BST + BA + GS ..	+++	++	+++	0	0		+++	++	++	0	
V	19	BST + SM	+++	+++	+++	−	+		+	+	+	0	+
	20	BST + SM + BA ..	+++	+++	+++	−	0		+++	+	+	0	+
	21	BST + SM + GS ..	+++	+++	++	0	0		+++	+	0	0	0

Abbreviations: BST, posterior biceps+semitendinosus nerve. SM, semimembranosus nerve. BA, anterior biceps nerve. Q, quadriceps nerve. S, sartorius nerve. GR, gracilis nerve. GS, nerve to lateral head of gastrocnemius+soleus. G, nerve to medial head of gastrocnemius. P, nerve to plantaris muscle. TA, nerve to anterior tibial muscle. FLD, nerve to flexor digit. long. muscle. GR and FLD not tested in all the experiments. For further explanations see the text.

mulation. The VSCT units were searched for under continuous stimulation, in experiments I and II, of the three hamstring nerves (the BST, the anterior biceps (BA), and the semimembranosus (SM) nerve) and the quadriceps (Q) nerve, and in experiments III—V, of the three hamstring nerves and the nerve to the soleus+lateral head of gastrocnemius (GS). Those nerves were stimulated which together evoked the largest mass discharge as that permitted identification of a maximal number of units. The third column in the table gives the nerve or nerves which had to be stimulated in order to evoke a postsynaptic discharge. Excitatory action from the various nerves is indicated with plus signs. Four pluses indicate that the VSCT unit could be discharged on stimulation of this nerve alone. Stimulation of nerves indicated with three pluses resulted in a postsynaptic discharge if two or, in some cases, three of them were stimulated in combination. The excitatory action from nerves indicated with one or two pluses was weak and could only be displayed as facilitation of the labile spike evoked from other nerves with stronger connection to the VSCT unit. Minus indicates inhibition and cipher no appreciable excitatory or inhibitory action.

It appears from the table that excitatory convergence is extensive whereas inhibition is uncommon. All units activated from one of the hamstring nerves were also activated from the others, as already described. These units usually also received excitatory action from the nerves to the medial head of gastrocnemius (G), the soleus+lateral head of gastrocnemius, and the plantaris (P). In addition facilitation often appeared from the gracilis (GR) and sometimes from the quadriceps nerve. One of the units (nr 13) received excitatory action from not less than 10 of the 11 dissected nerves.

Only three units were encountered which could be discharged from the quadriceps nerve. Two of these showed no or little convergence whereas the third (nr 9) received excitatory action from two of the hamstring nerves and also from the triceps nerve. As the quadriceps nerve belongs to more cranial segments than most of the nerves tested for convergence, it is not necessary to conclude that the "quadriceps units" receive less Ib

convergence than the "hamstring units". Possibly the "quadriceps units" receive Ib convergence from not dissected nerves.

Ib effects from the sartorius and the anterior tibial nerves were observed seldom or not at all.

All the units tabled above belong to the I-type (cf. Chapter I). Only a few E-units were examined completely and these showed a similar degree of convergence as the I-units.

In most of the experiments the ipsilateral hamstring nerve was prepared in addition to the contralateral nerves. More than 50 VSCT units were tested for group I effects from the ipsilateral nerve and none of them was appreciably influenced. It is concluded that the Ib effects to the VSCT neurons are strictly unilateral as are the group I effects to the DSCT neurons (HOLMQVIST et al. 1956).

In the not anaesthetized cat most of the encountered VSCT neurons could be discharged from one of the muscle nerves and not seldom from several nerves, but sometimes it was necessary to use combined stimulation of several nerves also in this type of preparation. In accordance with this finding the mass discharge was usually distinct on stimulation of a single muscle nerve. The discharge evoked from a flexor nerve was of the same magnitude as that evoked from an extensor nerve. Thus the discharges from the biceps p.+semitendinosus, the quadriceps, and the triceps nerves were of approximately the same magnitude.

DISCUSSION

The convergence of excitatory Ib action from different muscle nerves was found to be very extensive to most VSCT units. Although the pattern of convergence is diffuse some fairly constant features may nevertheless be discerned. Most of the encountered units belong to one of two groups, the first one receiving excitatory action from all the different hamstring nerves and the triceps nerve and usually also from the nerves to gracilis and plantaris. The second group consists of neurons discharged from the quadriceps nerve and usually receiving excitatory action also from the triceps nerve but not very often from the other dissected nerves.

The convergence of excitatory action from the nerves to posterior biceps+semitendinosus, semimembranosus, and anterior biceps was very marked and units activated from either of these nerves could usually be activated also from the other two. This is noteworthy as the posterior biceps and semitendinosus are flexor muscles, whereas the anterior biceps and semimembranosus are extensor muscles. This finding may possibly be correlated with the disclosure that the hip extensor motoneurons of the hamstring group are extensively Ia receptive from the knee flexors, the semitendinosus, posterior biceps, and gracilis (R. M. ECCLES and LUNDBERG 1957). However, in other aspects the pattern of the monosynaptic innervation of VSCT neurons bears no relation to that of the motoneurons. Likewise it deviates from that found for the DSCT which is characterized by a limited excitatory convergence (HOLMVQIST et al. 1956).

Inhibitory Ib action was found rather seldom. It was found most frequently in the units activated from the hamstring nerve, which rather often received inhibitory action from the quadriceps nerve. This cannot be taken as evidence for reciprocity, such as that found for the DSCT neurons or the motoneurons, as the units in question are activated not only from the posterior biceps+semitendinosus, the antagonist of the quadriceps, but also from the anterior biceps and the semimembranosus, which are extensors and not antagonists to the quadriceps. Neither were the units activated from the quadriceps nerve inhibited from the posterior biceps+semitendinosus nerve, but rather often facilitated from this nerve. In this respect the VSCT units differ markedly from the DSCT units which are characterized by reciprocal innervation from the group I afferents (LAPORTE et al. 1956 b, LUNDBERG and OSCARSSON 1956). In contrast to the VSCT, the DSCT is further characterized by a limited excitatory and a rather extensive inhibitory convergence (HOLMQVIST et al. 1956).

It may be enquired whether the pattern of convergence in the VSCT should be related to the segmental arrangement of the nerves. However, this is difficult to bring into accordance with the fact that the "hamstring units" often receive excitatory action from the gracilis but seldom from the quadriceps nerve

though both these nerves belong to the L V and L VI segments. Neither does it explain why the "quadriceps units" more often receive excitatory action from the triceps than from the hamstring nerves.

SUMMARY

The convergence of excitatory and inhibitory Ib effects onto VSCT neurons was investigated. The VSCT mass discharge and the discharge in single tract neurons were simultaneously recorded on stimulation of various muscle nerves in the hindlimbs.

The VSCT neurons receive extensive excitatory convergence from contralateral nerves. This convergence is not limited to Ib afferents of synergist muscles, and is often found from Ib afferents of antagonist muscles. Inhibitory Ib effects are found only occasionally. The pattern of convergence does not conform to the functional pattern of the muscles, and is different from that found in the dorsal spino-cerebellar tract and in the monosynaptic innervation of motoneurons.

Most of the encountered units belonged to one of two groups, the first one receiving excitatory action from all the different hamstring nerves and the triceps nerve, and usually also from the nerves to gracilis and plantaris. The second group consisted of neurons discharged from the quadriceps nerve and usually receiving excitatory action from the triceps nerve but not very often from the other dissected nerves. The first group rather often received inhibitory Ib action from the quadriceps nerve, but otherwise inhibition was seldom encountered.

No appreciable excitatory or inhibitory group I effects converge onto the VSCT neurons from ipsilateral nerves.

Chapter IV

Effects on electrical stimulation of muscle, joint, and skin nerves

A prominent mass discharge appears in the VSCT on stimulation of contralateral muscle nerves but no appreciable one on stimulation of skin nerves or ipsilateral muscle nerves (OSCARSSON 1956). The mass discharge is due to monosynaptic excitatory action from Golgi tendon organ afferents. In the present chapter it will be shown that, although no appreciable mass discharge is evoked on stimulation of other than contralateral muscle nerves, stimulation of skin, joint, and high threshold muscle nerve afferents strongly influences the VSCT. This may be displayed as inhibition or facilitation of the "Ib mass discharge" of the tract. The contralateral nerves are most effective in influencing the VSCT but fairly strong effects are obtained from the ipsilateral nerves.

RESULTS

1. Mass discharge recording

Record 1 in Fig. 15 shows the VSCT mass discharge evoked from the contralateral hamstring nerve and recorded from the dissected spinal half in the upper thoracic region. In records 2—4 the stimulus to the hamstring nerve is unchanged but preceded by supramaximal stimulation of the contralateral saphenus nerve. Stimulation of this nerve causes a longlasting potential due to activity in fibres not belonging to the VSCT (cf. OSCARSSON 1957 b, c). However, stimulation of the skin nerve in addition results in a marked decrease of the VSCT discharge. Even at an interval as long as 45 msec between the conditioning and testing stimuli (record 2) the tract discharge is very considerably reduced. In record 3 with a shorter interval the dis-

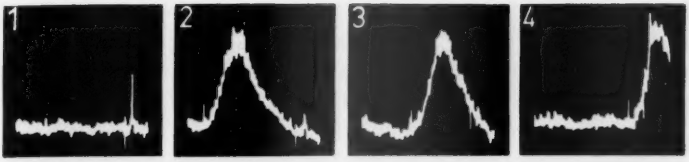


Fig. 15. Inhibition of VSCT mass discharge on stimulation of contralateral skin nerve. Record 1 shows the VSCT discharge recorded from the left dissected spinal half (except dorsal column) on maximal group I stimulation of the right hamstring nerve. Stimulation of the hamstring nerve unchanged in records 2—4 but preceded by supramaximal stimulation of the right saphenus nerve at different intervals. See text. Nembutal anaesthesia.

charge is hardly appreciable but reappears when the interval is further shortened as is shown in record 4. Usually the inhibition was complete or almost complete at a certain interval which varied from 15 to 25 msec in the different preparations. These values were obtained from anaesthetized animals. When the conditioning stimulus was applied to other contralateral skin nerves, such as the cutaneous peroneal or the sural nerve, the inhibition was as marked as from the saphenus nerve. Similar but weaker effects were obtained on stimulation of ipsilateral skin nerves.

Supramaximal stimulation of muscle and joint nerves resulted in similar effects as those obtained on skin nerve stimulation. This is illustrated in records 1—8 in Fig. 16. The test shock, slightly supramaximal to group I afferents, was delivered to the right hamstring nerve and the resulting VSCT mass discharge appears in the recording from the left dissected spinal half (upper beam). The lower beam, for comparison, shows the discharge in the DSCT recorded from the right dissected spinal half. The test discharges are shown in isolation in record 5. For conditioning, supramaximal shocks were delivered to the right posterior knee joint nerve (record 1), the right cutaneous peroneal nerve (record 2), and the right quadriceps nerve (record 3). In record 4 a conditioning supramaximal stimulus was evoked in the right hamstring nerve, *i. e.* the same nerve

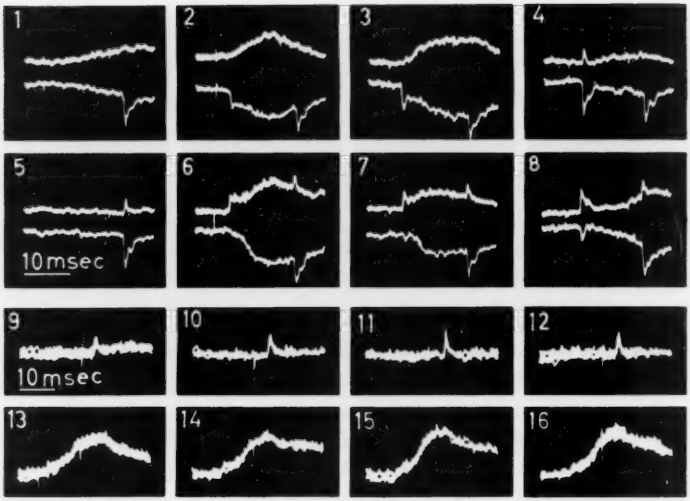


Fig. 16. Inhibition of VSCT mass discharge on supramaximal stimulation of various contralateral and ipsilateral nerves (records 1—8). Simultaneous recording from left (upper beam) and right (lower beam) dissected spinal halves (except dorsal columns) to show the VSCT and DSCT discharges. Conditioning with supramaximal stimulation of the right posterior knee joint nerve (record 1), the right superficial peroneal nerve at the ankle (record 2), the right quadriceps nerve (record 3), the right hamstring nerve (record 4), the left superficial peroneal nerve at the ankle (record 6), the left quadriceps nerve (record 7), and the left hamstring nerve (record 8). Testing with slightly supramaximal group I stimulation of the right hamstring nerve. Test discharges shown in isolation in record 5. Nembutal anaesthesia.

Records 9—16 were obtained from another preparation. Slightly supramaximal group I stimulation of the right quadriceps (record 9), semimembranosus (record 10), triceps (record 11), and biceps p.+semitendinosus (record 12) nerves. Corresponding lower records (13—16) obtained with unchanged stimulation of the muscle nerves but on conditioning with a supramaximal stimulation of the right saphenus nerve. Superposed sweeps. Nembutal anaesthesia.

as was used for testing. In all cases the VSCT discharge was almost completely inhibited. In contrast, the effects were small on the DSCT discharge. Records 6—8 were obtained with the test stimulus preceded by supramaximal stimulation of the left

cutaneous peroneal, the left quadriceps, and the left hamstring nerve respectively. The effects on the VSCT and DSCT discharges are hardly appreciable. The left joint nerve was not dissected, but the effect from the right nerve on the VSCT discharge evoked from the left hamstring nerve was very small.

In experiments with several contralateral muscle nerves prepared (those listed in Table 3, p. 43), complete or almost complete inhibition of the VSCT mass discharge could be obtained from all of them on supramaximal stimulation.

Similar effects on the VSCT mass discharge were obtained when a flexor and an extensor nerve was used for testing. Records 9—12 show in succession the test discharges on stimulation of the contralateral quadriceps, triceps, biceps p.+semitendinosus, and biceps a.+semimembranosus nerves. The corresponding lower records (13—16) show the effects on conditioning with a volley from the contralateral saphenus nerve. The VSCT discharge is almost completely abolished in all the cases.

The time course of the conditioning effects from the various nerves was examined in five experiments on cats under nembutal anaesthesia. The anaesthetized preparation has the advantage that the test volley to the VSCT leaves a large undischarged subliminal fringe which may be used to disclose excitatory action as facilitation. The VSCT discharge evoked from the right hamstring nerve was used for testing the effects of preceding supramaximal stimuli to the right and left hamstring, posterior knee joint, and saphenus nerves. The amplitude of the conditioned VSCT discharge was plotted in per cent of the amplitude of the unconditioned discharge against the time interval between the conditioning and testing volleys. The curves obtained from a representative experiment are shown in Fig. 17. Conditioning with supramaximal stimulation to the right hamstring nerve resulted in inhibition which became maximal after about 20 msec and then gradually decreased (curve 1, circuits). The inhibition was converted into facilitation after about 85 msec. This became maximal after 150 msec and then declined to zero after 300 msec. These effects were due to impulses in high threshold afferents as stimulation of group I affe-

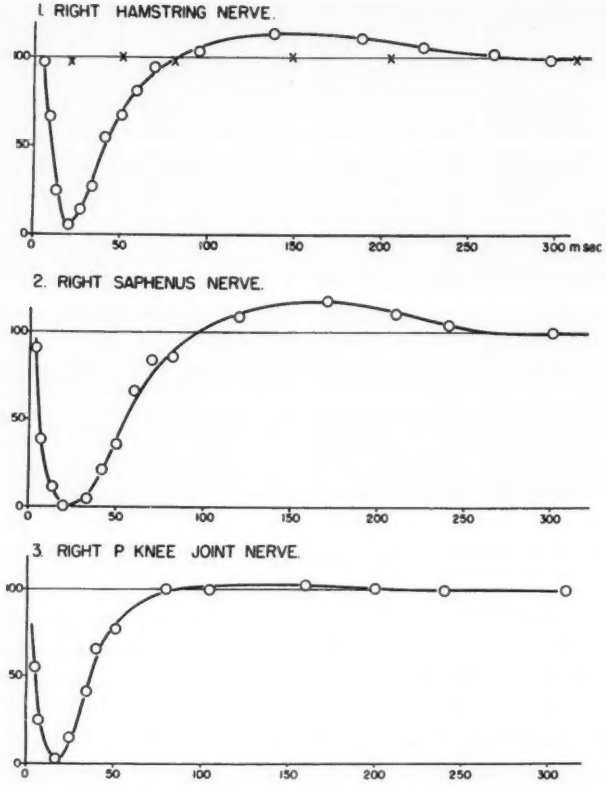
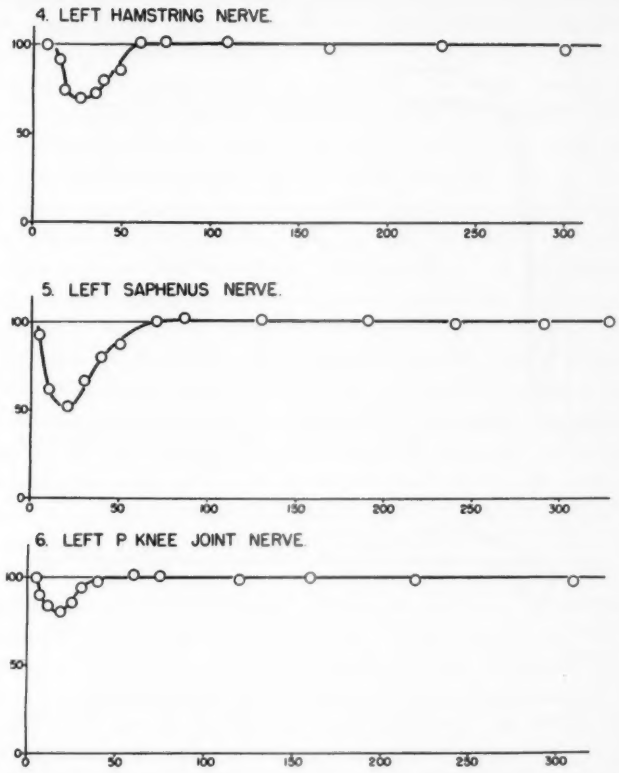


Fig. 17. Time course of effect of supramaximal stimulation of contralateral and ipsilateral muscle, skin, and joint nerves on VSCT mass discharge. Nembutal anaesthesia. Abscissa: interval between conditioning and testing volleys. Ordinate: amplitude of conditioned VSCT discharge in per cent of amplitude of unconditioned one. Test discharge evoked from the right

rents did not result in any noticeable effects (curve 1, crosses). Conditioning with a stimulus to the saphenus nerve gave similar though slightly stronger effects, as is shown in curve 2. Joint nerve stimulation (curve 3) resulted in almost complete inhibition as did muscle and skin nerve stimulation, but the facilitation was insignificant. Conditioning from the left nerves gave



hamstring nerve. Conditioning by supramaximal stimulation of the contralateral (right) and ipsilateral (left) hamstring nerve, saphenus nerve, and posterior knee joint nerve. Curve 1 also shows effect on conditioning with a group I volley in the right hamstring nerve (crosses). All points represent average of about 15 separate recordings.

comparatively small effects and no appreciable facilitation followed the inhibition (curves 4—6).

The results from the other experiments were in good conformity with those illustrated by the curves in Fig. 17. The inhibition from contralateral nerves was maximal after 15 to 25 msec and almost complete in all the experiments. The con-

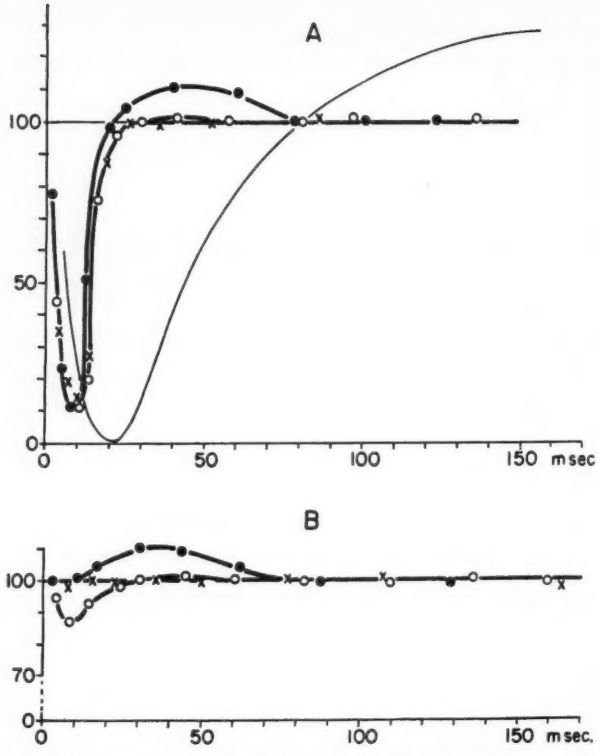


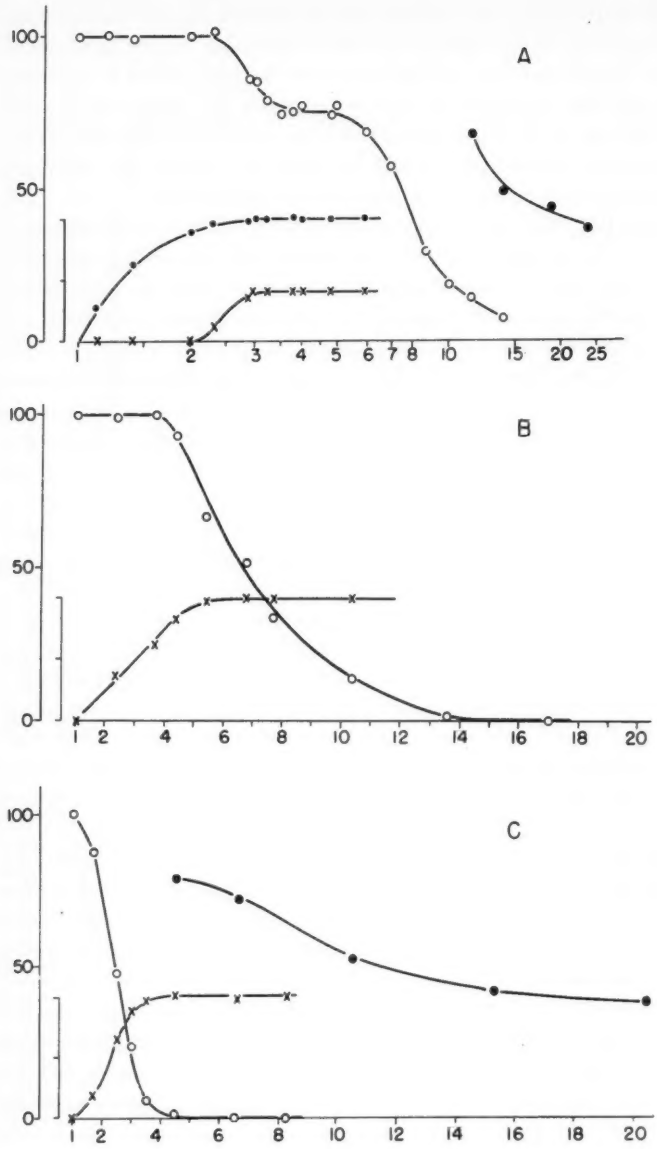
Fig. 18. Time course of effect of supramaximal skin nerve stimulation on VSCT mass discharge in not anaesthetized preparation. Abscissa: interval between conditioning and testing volleys. Ordinate: amplitude of conditioned VSCT mass discharge in per cent of unconditioned one. Test discharge evoked from right hamstring nerve. Conditioning by supramaximal stimulation of right (A) and left (B) superficial peroneal nerve at the ankle. Results from three different experiments indicated with different symbols. All points represent average of about 15 separate recordings. For comparison the time course in the anaesthetized preparation is shown (thin line in A).

version from inhibition to facilitation occurred after 75 to 100 msec, and the succeeding facilitation reached its maximum after about 150 msec and then declined to zero after 250 to 300 msec. The facilitation was marked on stimulation of muscle

and skin nerves and varied between 10 and 55 per cent but was very small or not appreciable on stimulation of the joint nerve. The inconsiderable facilitation from the joint nerve is probably completely explained as due to the small size of the nerve. The inhibition from the ipsilateral nerves varied considerably in the different experiments, being between 15 and 65 per cent, and was not followed by any appreciable facilitation.

Similar experiments were also performed on not anaesthetized cats. Three experiments were made and the curves obtained on skin nerve conditioning are shown in Fig. 18. The curves obtained on muscle and joint nerve conditioning showed corresponding deviations from those illustrated in Fig. 17. The VSCT mass discharge in the not anaesthetized animal is without, or almost without, subliminal fringe (Chapter II). This makes excitatory action difficult or impossible to judge. The curves obtained on contralateral conditioning were similar in all the three experiments (Fig. 18: A). The VSCT discharge was inhibited as in the anaesthetized animal, but the inhibition reached its maximum earlier and lasted for a shorter period. The short duration is probably due to a rapidly ensuing facilitation, overlapping and counteracting the inhibition. In one of the experiments (filled circuits) the subliminal fringe was large enough to display facilitation and this actually showed up already after about 25 msec. The inhibition was not complete in any of the experiments. This is not due to a weaker inhibitory effect than that found in the experiments on anaesthetized cats, but is well accounted for by the existence of E-units. These are facilitated at short intervals between the conditioning and testing volleys but inhibited at longer intervals (see below). The maximal inhibition of the VSCT discharge in the not anaesthetized animal occurs at an interval when most E-units are facilitated, whereas in the anaesthetized animal at an interval when most are inhibited.

The facilitation displayed in one of the curves in Fig. 18: A has a shorter duration than the facilitation obtained in anaesthetized cats. This may partly be due to the small subliminal fringe which makes it difficult to assess a small facilitation, but evidently the time course is quite different from that in the anaesthetized animal.


A
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16
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20

The results on contralateral conditioning varied much more than those on ipsilateral conditioning (Fig. 18: B). In one of the experiments there was a small inhibition of similar time course as that appearing on contralateral conditioning (open circuits). In the other two experiments no inhibition was observed. No appreciable effect at all was observed in one of them (crosses), but in the other there was a marked facilitation (filled circuits). This began already after about 10 msec. In the latter experiments the inhibition was probably concealed by a more or less simultaneous facilitation. It will be shown that on adequate stimulation of skin receptors effects are obtained which correspond to those obtained on electrical stimulation (Chapter V).

From the experiments described above it appears that the VSCT was more or less strongly influenced from all the tested hindleg nerves. It was thought possible that clues to the functional significance of this extensive convergence might be obtained if the effects could be related to certain components of the afferent fibre spectrum in the various nerves. In order to do that the inhibition from contralateral nerves was correlated

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Fig. 19. Electrical threshold of afferents causing inhibition of VSCT discharge. Abscissa: strength of conditioning stimulus with threshold for just appreciable ingoing volley as unit. Logarithmic scale in curve A and linear scales in curves B and C. Outer ordinate: amplitude of conditioned VSCT discharge in per cent of unconditioned one. Inner ordinate represents amplitude of ingoing volley in per cent of maximal value. *Curve A* obtained on conditioning with stimulation of the right hamstring nerve and testing with combined stimulation of the right quadriceps and triceps nerves. Ingoing volley judged from recording of coarse L VII dorsal root filament and shown as amplitude of the group I volley (dots) and amplitude of the group II volley (crosses). Interval between conditioning and testing volleys 18 (open circuits) and 30 msec (filled circuits). The group I of the ingoing volley did not increase at high stimulation strengths (not shown). *Curve B* obtained on conditioning with stimulation of the right posterior knee joint nerve and testing with stimulation of the right hamstring nerve. Ingoing volley judged from recording of the joint nerve about half a cm proximally of the stimulating electrode. Interval about 18 msec. *Curve C* obtained on conditioning with stimulation of the right superficial peroneal nerve at the ankle and testing with stimulation of the right hamstring nerve. The amplitude of the ingoing volley did not increase at high stimulation strengths (not shown). Interval about 18 (open circuits) and 35 msec (filled circuits). Nembutal anaesthesia.

to stimulus strength and ingoing primary afferent volley. A conditioning stimulus of increasing strength was applied to the nerve to be studied, and its effect was examined on the VSCT discharge. The interval between the conditioning and testing volleys was adjusted to give maximal inhibition.

It was noted in the previous experiments (cf. Fig. 17) that the inhibition and succeeding facilitation from muscle nerves appeared only on stimulation supramaximal to group I. The result of a more detailed investigation is shown in Fig. 19: A. The conditioning stimulus was delivered to the hamstring nerve and the ingoing volley judged from a dissected dorsal root filament. The effect of the conditioning stimulus was tested on the VSCT discharge evoked on combined stimulation of the quadriceps and triceps nerves. The VSCT discharge begins to decrease when the stimulus strength is increased to 2.4 times the threshold value. At a strength of 3.5 the discharge is about 75 per cent of the unconditioned discharge. On further increase of stimulus strength the inhibition flattens out and a plateau is formed. A second phase of inhibition sets in when the stimulus is increased to about 5.0 times threshold and on further increase the VSCT discharge gradually diminishes. In order to test the effect from high threshold afferents, the interval between the testing and conditioning stimuli was increased and part of the experiment repeated (filled circuits). That the inhibition was not partly due to stimulus escape was checked by judging the ingoing group I volley which did not increase (not shown in the figure).

The first phase of inhibition coincides well with the appearance in the dissected root filament of the group II volley and its growth to maximum. The next decrease of the discharge is probably due to stimulation of group III afferents. The group III volley could not be discerned in the filament recording but the strenght, at which the second phase of inhibition sets in, is in good agreement with the value for the threshold of group III fibres assessed by Brock, Eccles, and Rall (1951). The inhibition increases further with high stimulation strengths.

Two similar experiments were performed with both conditioning and testing stimuli applied to the same nerve, the

hamstring nerve. Very similar curves were obtained. Thus, in one of the experiments, the first decrease of the mass discharge appeared at a strength of about 2.2 times threshold and the second at 4.0 times threshold. The plateau was at 80 to 85 per cent of the unconditioned discharge. In these experiments the contingency of the first part of the inhibition being partly due to refractoriness of the previously discharged VSCT neurons could not be definitely excluded. In order to evade this possibility the experiment described above was devised. However, there is usually no appreciable depression of the VSCT discharge after antidromic or homosynaptic conditioning (cf. Chapter II and also Fig. 17: 1) and furthermore the curves obtained were very similar. It is concluded that group II afferents contribute to the inhibition of the VSCT discharge but that stronger inhibitory effects are obtained from afferents of higher threshold.

The inhibition evoked from the knee joint nerve was examined in three experiments which all gave consistent results. The curve in Fig. 19: B was obtained from one of the experiments. The input volley was recorded from the joint nerve half a centimetre proximally of the stimulating electrodes (cf. OSCARSSON 1957 c) and is plotted on a separate ordinate. No decrease of the VSCT discharge was observed before the stimulus was increased to more than 4 times threshold, when the recorded volley was about 80 per cent maximal, and most of the inhibition appeared after the volley had reached its maximal amplitude. It is concluded that the low threshold joint nerve afferents which are known to arise from receptors signalling position and movement in the joints (cf. SKOGLUND 1956) do not appreciably influence the VSCT. Evidently the inhibition is due to high threshold afferents which contribute little or nothing to the amplitude of the input volley.

Fig. 19: C shows the effect of skin nerve stimulation. The inhibition appears already at a very weak stimulus strength, and the inhibition is practically complete before the amplitude of the input volley is maximal. In order to test effects from fibres of higher threshold, the interval was increased and part of the experiment repeated (filled circuits). There is a further decrease of the discharge at high stimulation strengths. In con-

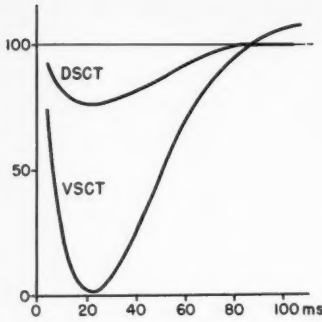


Fig. 20. Comparison of effect of skin nerve stimulation on DSCT and VSCT mass discharges. Tract discharges evoked from right hamstring nerve. Skin nerve effect obtained by supramaximal stimulation of right saphenus nerve. Ordinate: amplitude of conditioned tract discharge in per cent of amplitude of unconditioned one. Abscissa: time interval between testing and conditioning ingoing volleys. The curves were obtained as those shown in Fig. 17. Nembutal anaesthesia.

trast to the inhibition from muscle and joint nerves, the inhibition appearing on skin nerve stimulation is mainly due to low threshold afferents though also high threshold afferents do contribute.

The facilitation which follows the inhibition was not especially investigated but on recording from single units the inhibitory and facilitory effects were observed to appear concomitantly, and it seems probable that the whole sequense of late effects is due to the same categories of afferents.

Effects in the dorsal spino-cerebellar tract. The effect of skin nerve stimulation on the DSCT and VSCT discharge was compared in the experiment illustrated in Fig. 20. As described above the VSCT discharge is first strongly inhibited and later facilitated. The DSCT discharge is also inhibited but to a lesser degree than the VSCT discharge. The inhibition has a similar time course in both tracts. No appreciable facilitation follows the inhibition of the DSCT discharge which may possibly be due to the small subliminal fringe in the DSCT.

Similar effects were also evoked on supramaximal stimulation of muscle and joint nerves. The DSCT mass discharge evoked from the right hamstring nerve was conditioned by stimulation of the right posterior knee joint, superficial peroneal, quadriceps, and hamstring nerves. This resulted in a depression of the DSCT mass discharge of 7, 25, 24, and 14 per cent respectively. Weaker effects were obtained on conditioning by stimulation of the left (contralateral) superficial peroneal, quadriceps, and hamstring nerves, *viz.* a depression of 11, 7, and 7 per cent. These results were obtained from the experiment illustrated in Fig. 16, each value being the mean of 10—15 observations.

2. Single unit recording

The effects from different nerves were also examined in single units. The hamstring, cutaneous peroneal, and posterior knee joint nerves were dissected for stimulation bilaterally. More than 80 VSCT units (10 experiments) activated monosynaptically from Ib afferents in the right hamstring nerve were examined on supramaximal stimulation of the various nerves. The experiments on single units confirmed the results obtained on mass discharge recording, but the behavior of the units was found to vary considerably. This was especially marked in unanaesthetized preparations. First the effects on VSCT units of I-type will be described. These units are defined as responding with a single spike on supramaximal stimulation of contralateral muscle nerves (Chapter I). The I-units constitute about 90 per cent of the VSCT units identified from the hamstring nerve.

A. *I-units*

In the anaesthetized animal the I-units usually are silent and the effects were tested with a "labile" spike evoked on weak stimulation of the right hamstring nerve. Inhibition could regularly be displayed from all the nerves of the right side but only in about half the number of units from those of the left side. The inhibition usually appeared after 5—10 msec but was sometimes apparent already after 2—3 or only after 15—25 msec. The duration varied from 10 to several hundreds of msec. The time course was, however, for the same unit, similar on stimulation of all the nerves of one side. It was rather often possible to display late facilitory effects and in some units one or two spikes appeared after a very long latency in the otherwise silent unit. These units are nevertheless classified as I-units in accordance with their general behavior. Such a unit is shown in Fig. 21. Record 1 was obtained on supramaximal stimulation of the right hamstring nerve. The first spike is due to the Ib excitatory action whereas the second one appears only on supramaximal group I stimulation. It has a latency of about 85 msec. Records 2—5 were obtained with a slightly faster sweep speed. Record 2 again shows stimulation of the hamstring nerve. With

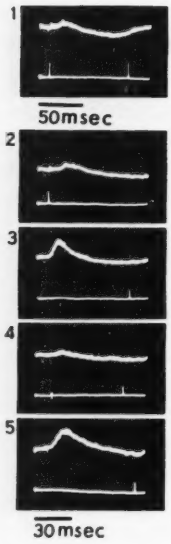


Fig. 21. Late facilitation in VSCT unit of I-type. Simultaneous recording from left dissected spinal half (except dorsal column) and from VSCT fibre in left ventro-lateral funiculus on supramaximal stimulation of the right hamstring nerve (records 1 and 2), the right superficial peroneal nerve at the ankle (record 3), the right posterior knee joint nerve (record 4), and the left superficial peroneal nerve at the ankle (record 5). Nembutal anaesthesia.

this sweep speed the second spike falls out of the screen. As is shown in records 3 and 4 spikes appeared also on stimulation of the right skin and joint nerves. Stimulation of the left skin nerve resulted in a late spike (record 5), but no activity was evoked on stimulation of the other left nerves.

The effects in the unanaesthetized preparation were much easier to appreciate as the units usually were spontaneously active. As in the anaesthetized cat stimulation of the right nerves resulted in inhibition. This inhibition was sometimes followed by a more or less marked facilitation. As a rule the effects were very similar from all the nerves. However, as could be expected, the effects were often somewhat stronger from the skin nerve and somewhat weaker from the joint nerve. Three units are illustrated in Fig. 22. In the unit shown in A a pause of about 50 msec's duration was obtained on stimulation of the contralateral (right) nerves. This pause was not followed by any appreciable facilitation. No certain effects were obtained from the ipsilateral nerves. B shows a unit which was inhibited

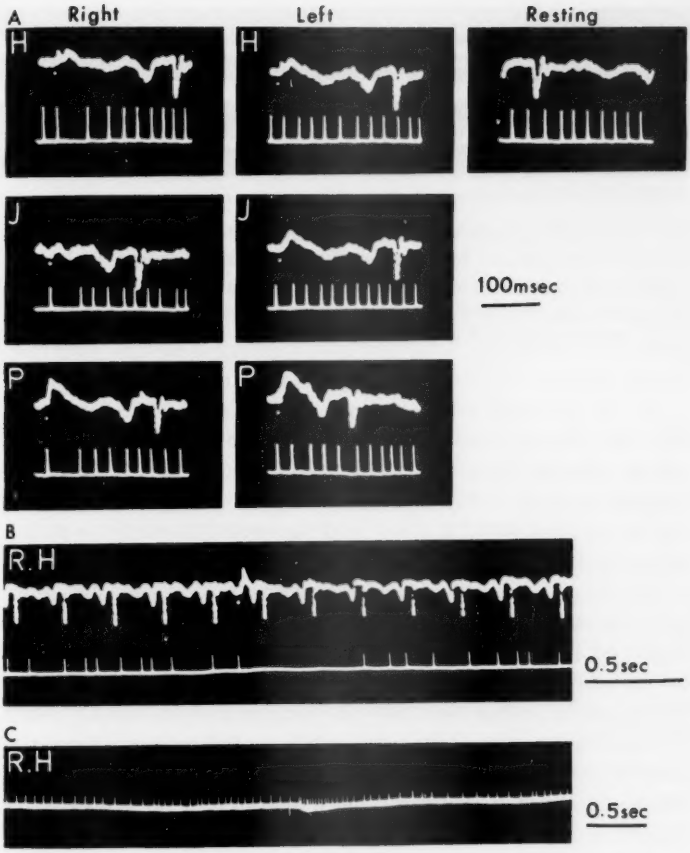
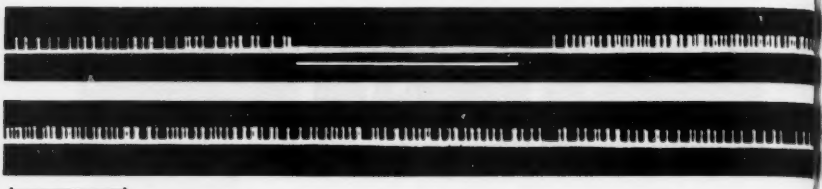


Fig. 22. Late effects in three different VSCT units of I-type (A, B, and C). Unanaesthetized preparation. *A.* Simultaneous recording from left dissected spinal half (except dorsal column) and VSCT fibre in left ventro-lateral funiculus on supramaximal stimulation of right and left hamstring nerves (H), posterior knee joint nerves (J), and superficial peroneal nerves at the ankle (P). Right upper record obtained under resting conditions. White dots mark stimulus artefacts. Mass discharge recording distorted by electrocardiogram. *B.* Recording as in A. Supramaximal stimulation of the right hamstring nerve (R. H.). White dot marks shock artefact. Mass discharge recording distorted by electrocardiogram. *C.* Recording from VSCT fibre in left ventro-lateral funiculus on supramaximal stimulation of the right hamstring nerve.



1 sec

Fig. 23. Effect of supramaximal tetanic stimulation of contralateral skin nerve in VSCT unit of I-type. This VSCT unit was discharged by Ib afferents in the contralateral hamstring nerve. White line indicates tetanic stimulation of the contralateral superficial peroneal nerve at the ankle. Upper record continued without interruption in lower record. Unanaesthetized preparation.

for more than 600 msec on stimulation of the right hamstring nerve. Stimulation of the right skin and joint nerves displayed inhibitory actions of similar lengths. C shows a unit which was inhibited for about 100 msec and then accelerated for a period of several hundred msec.

The effects from the ipsilateral nerves were weaker and more varying than the effects from the contralateral ones. In some units, as in the one shown in 22: A, no appreciable effect was observed, in others a very short pause was followed by a marked acceleration, and in two units the acceleration appeared at once.

Repetitive supramaximal stimulation of the dissected contralateral skin and joint nerves always caused inhibition. Fig. 23 shows a VSCT unit which was discharged on group I stimulation of the contralateral hamstring nerve. Repetitive stimulation of the cutaneous peroneal nerve completely silenced the unit. At the end of the stimulation the unit remains silent for some hundreds of msec, and then an acceleration follows with a duration of several seconds. Such a late rebound was often observed and may possibly be correlated to the late facilitation often found on single shock stimulation. Repetitive supramaximal stimulation of the contralateral hamstring nerve sometimes resulted in acceleration due to the Ib effects but often in inhibition similar to that obtained on stimulation of the contralateral skin and joint nerves. Repetitive stimulation of the

ipsilateral nerves sometimes evoked inhibition but more often facilitation shown as acceleration of the resting discharge. In the latter cases evidently the late facilitory effect dominated.

B. *E-units*

Only about 10 E-units were encountered but these all conformed to a general pattern. When the stimulation of the contralateral muscle nerve was increased to slightly supramaximal for group I, further spikes appeared. In some of the units spikes appeared already before the group I volley was completely maximal. The threshold for and latency of these spikes suggest that they are due to group II afferents (cf. Fig. 3, p. 15). Afferents of higher threshold also contribute as sometimes further spikes were evoked on considerably increased stimulus strength.

The E-units receive excitatory action from skin and joint nerves as shown in Fig. 24. Records 1, 2, 6, and 7 are shown for identification. Record 1 shows the "Ib spike" on slightly submaximal group I stimulation of the right hamstring nerve. Further spikes appear in record 2 with the stimulus strength increased to supramaximal. Record 6 shows the latency of the "Ib spike" on a faster sweep, and record 7 the antidromic spike obtained on stimulation of the dissected spinal half. Record 3 was obtained on stimulation of the right cutaneous peroneal nerve which evoked a discharge of four spikes. Two spikes appeared on stimulation of the right joint nerve (record 4). Of the left nerves only stimulation of the skin nerve resulted in a discharge of the unit (record 5). Regularly all the right nerves and often also the left nerves evoked spike activity in the E-units.

Fig. 25 shows another E-unit. Record 1 was obtained under resting conditions. Record 2 shows the early spike activity due to supramaximal stimulation of the right hamstring nerve. This is followed by a pause of about 80 msec's duration. Supramaximal stimulation resulted in the appearance of one to three further spikes in this unit. That the pause is not due to refractoriness is shown in the next record in which only one spike was evoked. In spite of this the succeeding pause is as long as in the previous record. Furthermore, a similar pause appeared

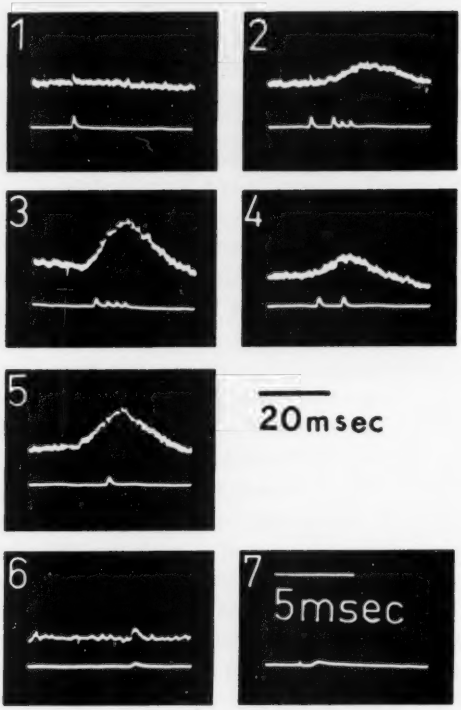


Fig. 24. Convergence of excitatory effects from various nerves onto VSCT unit of E-type. Simultaneous recording from left dissected spinal half (except dorsal column) and from VSCT fibre in left ventro-lateral funiculus (records 1—6). Record 1 obtained on slightly submaximal group I stimulation and record 2 on supramaximal stimulation of the right hamstring nerve. Supramaximal stimulation of the right superficial peroneal nerve at the ankle (record 3), right posterior knee joint nerve (record 4), and left superficial peroneal nerve at the ankle (record 5). Record 6 obtained on stimulation as in record 1 but on a faster sweep to show the latency of the orthodromic spike. Record 7 shows the antidromic spike on stimulation of the dissected spinal half. Distance dissected spinal half—site of micro-electrode recording 7.2 cm. The action potential was partially blocked in the neighbourhood of the micro-electrode causing a hump in the spike (records 1—5), and later completely blocked (records 6 and 7) (cf. WOODBURY 1952). Unanaesthetized preparation.

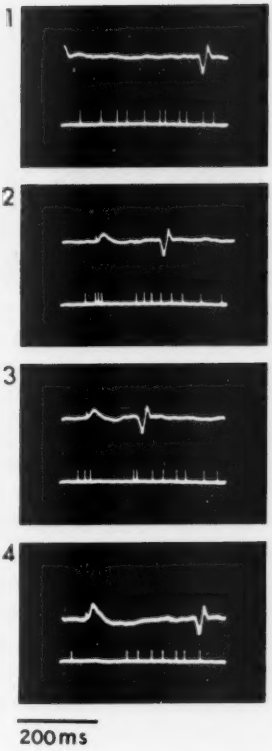


Fig. 25. Late inhibitory and facilitory effects in VSCT unit of E-type. Simultaneous recording from left dissected spinal half (except dorsal column) and VSCT fibre in left ventro-lateral funiculus. Record 1 obtained under resting conditions. Records 2 and 3 obtained on supramaximal stimulation of the right hamstring nerve. Record 4 obtained on supramaximal stimulation of the left hamstring nerve. Mass discharge recording distorted by electrocardiogram. Unanaesthetized preparation.

on supramaximal stimulation of the left hamstring nerve (record 4) in which case no preceding facilitation was evident. A similar inhibitory action was also found in other E-units and is probably a constant feature. In records 2 and 3 in Fig. 25 a slight acceleration follows the inhibition. Such an acceleration was not constant but sometimes discerned. These findings strongly suggest that the I- and E-units only differ in that the sequence of inhibitory and facilitory effects, found in the I-units, in the E-units are preceded by a strong short-lasting excitatory action.

In some of the E-units the effect of tetanic stimulation was examined and found to be acceleration of the resting discharge.

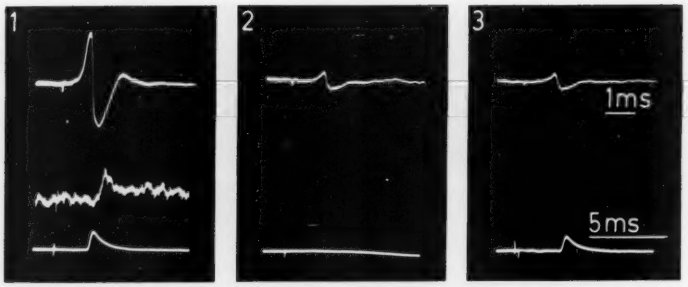


Fig. 26. Facilitation of VSCT unit on stimulation of contralateral dissected spinal half. Simultaneous recording from right L VII dorsal root entry zone (upper beam), from dissected left spinal half (except dorsal column) (middle beam, only in record 1) and from VSCT fibre in left ventrolateral funiculus (lower beam). Record 1 obtained on maximal group I stimulation of the right hamstring nerve. Record 2 on weak stimulation of this nerve which did not evoke a spike in the unit. Record 3 was obtained with unchanged hamstring nerve stimulation but on conditioning with stimulation of the right dissected spinal half (except dorsal column). Nembutal anaesthesia.

The threshold of the joint and skin nerve afferents which evoked spiking activity in the E-units was judged from the ingoing volley or from the mass discharge in the dissected spinal half. On stimulation of the skin nerve spikes appeared already with low threshold afferents but on stimulation of the joint nerve only with high threshold afferents. It seems probable that the effects are evoked from the same combination of afferents which was described in the previous section, namely high threshold muscle and joint nerve afferents and low and high threshold skin nerve afferents.

3. Facilitation evoked on stimulation of the dissected contralateral half of the spinal cord

VSCT units identified as monosynaptically discharged on stimulation of low threshold afferents in the contralateral hamstring nerve were examined for effects on stimulation of the contralateral dissected spinal half. Of the 35 units encountered (4 experiments) 24 were influenced on such sti-

mulation. In all cases the effect was facilitation as is illustrated in Fig. 26. Record 1 was obtained on maximal group I stimulation of the hamstring nerve and shows the ingoing volley recorded from the L VII dorsal root entry zone, the VSCT mass discharge, and the spike appearing in the VSCT unit. Record 2 was obtained on a weaker stimulation which did not discharge the unit. The same stimulus strength, however, evoked a spike if preceded by stimulation of the dissected spinal half as shown in record 3.

Usually the facilitory effect was weak but in some cases rather strong. One unit was actually discharged on isolated stimulation of the contralateral spinal half. The latency of the spike was about 3.5 msec. The facilitation was most marked when the conditioning stimulus was delivered to the spinal half slightly previous to the testing stimulus of the hamstring nerve. Weak facilitation could often be displayed at intervals up to 5—10 msec.

In one of the experiments it was shown that the facilitation remained after sectioning of the dorsal columns and the contralateral Flechsig's fasciculus. This suggests that the fibres causing the facilitation are localized to the ventral quadrant of the spinal cord. The conduction velocity was not assessed but the latency was about the same as for the excitatory action on stimulation of the hamstring nerve. As the presynaptic pathways were of approximately the same length this indicates that the conduction velocity must be considerable. It also suggests that the connection is monosynaptic.

The facilitation may be due to collaterals of ascending fibres but another possibility is that it is due to a special system of descending fibres controlling the discharge niveau of the VSCT neurons. Such a centrifugal control has been demonstrated in other sensory pathways (cf. HAGBARTH and KERR 1954, GRANIT 1955a, KERR and HAGBARTH 1955, DODT 1956, GALAMBOS 1956). All the examined units were of I-type and in these units an excitatory bias may be of special importance as the message probably is coded as inhibition (Chapter V) necessitating the maintenance of a resting discharge as background.

DISCUSSION

The present investigation has shown that the VSCT neurons are strongly influenced from high threshold muscle and joint nerve afferents and low and high threshold skin nerve afferents. The different categories of fibres cause almost identical effects when evoked on stimulation of contralateral nerves and similar but weaker effects when evoked from ipsilateral nerves. Each VSCT neuron may be influenced from probably all muscle, joint, and skin nerves of the hindlimbs indicating a very extensive spatial convergence.

It may be argued whether the convergence of effects from the various afferents onto the VSCT neurons may to some part be due to the dorsal root reflex which at least under certain experimental conditions may be provoked on stimulation of both skin and muscle nerves (TOENNIES 1938, 1939, BROOKS and KOIZUMI 1956). The dorsal root reflex is very small at a normal body temperature but large at subnormal temperatures (BARRON and MATTHEWS 1938, TOENNIES 1939, BROOKS and KOIZUMI 1956). In contrast the effects from the various nerves converging onto the VSCT neurons are very strong already at a normal body temperature and are not appreciably increased when the temperature is lowered from 39° to 36° C. In the next chapter it will be shown that one VSCT unit may receive excitatory action from one nerve and inhibitory action from another. Such diverse effects indicate separate pathways from different peripheral nerves to the VSCT neurons and are incompatible with the possibility that the dorsal root reflex is of any major importance for the convergence onto these neurons. In that chapter it will also be shown that weak adequate stimulation of muscle and skin receptors evokes the effects to be expected from the present experiments with electrical stimulation of severed nerves. These findings give further support to the assumption that the convergence observed on electrical stimulation reflects a normal functional pattern.

It is of interest that a similar combination of primary afferents, as those converging onto the VSCT neurons to give the late effects, also have been found to converge onto neurons belonging to other ascending spinal tracts. LAPORTE et al.

(1956 b) showed that some neurons in Flechsig's fasciculus were discharged from both skin afferents and high threshold muscle nerve afferents. It has later been shown (OSCARSSON 1957 b, c) that these neurons receive excitatory action from high threshold joint nerve afferents as well, and that the receptive field for all these actions is ipsilateral. Another pathway, localized to the ventro-lateral quadrant of the spinal cord, receives a similar type of convergence from both ipsilateral and contralateral nerves (OSCARSSON 1957 b, c). Both these pathways do not receive any appreciable effects from low threshold muscle and joint nerve afferents.

SUMMARY

Recording was performed from the dissected spinal half for evaluating the VSCT mass discharge and from single VSCT fibres on electrical stimulation of various nerves in the hindlimbs.

In addition to the effects from Golgi tendon organ afferents, described previously, the VSCT neurons receive strong effects from afferents of higher threshold than group I in muscle nerves, and from afferents in joint and skin nerves. The latter effects, as revealed on supramaximal (for A fibres) stimulation of contralateral muscle, joint, and skin nerves, result in strong inhibition often followed by a late facilitation of the I-units. Similar but weaker effects are obtained from the ipsilateral nerves. The effects on the E-units are similar, but in these units the inhibition is preceded by a strong short-lasting excitatory action.

The effects from the various nerves were correlated to electrical threshold and ingoing volley of the primary afferents. The effects on increasing muscle nerve stimulation appear with the group II afferents but are mainly due to afferents of higher threshold. The effects from joint nerves are due to high threshold afferents, whereas the skin nerve effects are due to both low and high threshold afferents.

Some of the VSCT neurons were facilitated on electrical stimulation of the contralateral dissected spinal half. This facilitation may be due to collaterals of ascending fibres or to descending fibres controlling the discharge niveau of the VSCT neurons.

Chapter V

Effects on adequate stimulation of various receptors

Previously the VSCT mass discharge and the response of single VSCT neurons was studied on electrical stimulation of severed nerves. An appreciable discharge in the VSCT is recordable only on stimulation of contralateral muscle nerves. This discharge is well synchronized and due to monosynaptic excitatory action from contralateral Golgi tendon organ afferents. The mass discharge is, however, influenced by stimulation of other afferents than Ib afferents. Stimulation of skin nerve afferents and high threshold muscle and joint nerve afferents results in effects which may be displayed as inhibition or facilitation of the mass discharge. In the present chapter it will be shown that the behaviour of the VSCT neurons on adequate stimulation of various receptors is dominated by the effects from skin and high threshold muscle nerve afferents, and that the monosynaptic excitatory action from Golgi tendon organ afferents is of little, or no, functional significance.

RESULTS

1. Adequate stimulation of muscle receptors

Adequate stimulation of muscle receptors might be expected to influence the VSCT neurons both through effects from Ib afferents and effects from high threshold muscle nerve afferents. The Ib effects are mainly excitatory, and strong effects to a certain VSCT neuron are limited to the afferents from one or a few contralateral muscle nerves. In contrast, the effects from high threshold afferents are exerted from a wide range of nerves. On electrical stimulation such effects may be provoked from all the muscle nerves of the contralateral hindlimb and usually also from those of the ipsilateral one.

METHODS. The preliminary experiments were performed on cats under nembutal anaesthesia. In the later experiments only unanaesthetized decerebrate cats were used in order to avoid the depressant effect of anaesthesia on the connection between Ib afferents and VSCT neurons (Chapter II). Similar results were obtained from both types of preparations and only those obtained from not anaesthetized animals will be described. Most of the cats were spinalized at the upper thoracic region for dissecting the spinal cord for recording the VSCT mass discharge. Some cats were not spinalized in order to make it possible to study the effects in a decerebrate preparation.

The VSCT units were identified as units monosynaptically activated from contralateral group Ib afferents. In the spontaneously active VSCT units the effects of adequate stimulation were judged by the acceleration or decceleration of the resting discharge. In silent neurons the effects were tested with a "labile" spike evoked by weak electrical stimulation of the nerve supplying Ib excitatory action.

In most experiments the hamstring nerve was severed and used for identification of VSCT neurons together with the triceps and quadriceps nerves which, however, were in intact connection with their muscles. In a few experiments also the semitendinosus muscle was used. In these cases the semitendinosus (+severed biceps p.) nerve was used for identification instead of the whole hamstring nerve. The rest of the contralateral hindlimb was denervated as was the ipsilateral one except in two experiments in which the triceps and quadriceps muscles were prepared bilaterally. The tendons of the muscles to be used for adequate stimulation were freed from their insertions and could be pulled by hand or connected to an isometric myograph.

In some experiments, especially designed to provoke strong effects from Golgi tendon organs, the triceps muscle was prepared and stimulating electrodes applied to the triceps nerve for identification of VSCT units monosynaptically activated from this nerve. A laminectomy was performed in the lower lumbar region. The L VII and S I ventral roots were severed and the peripheral ends mounted on electrodes for stimulation of the efferent fibres in order to cause contraction of the triceps muscle. An electrical heater was arranged around the leg in order to keep the muscle warm. The temperature of the muscle was checked during the experiments and varied within 36.5 and 38.5° C.

A. *Effects from muscles without, or with only weak, Ib connection to the investigated neuron*

VSCT units, monosynaptically discharged from Ib afferents in the hamstring nerve but not from Ib afferents in the quadri-

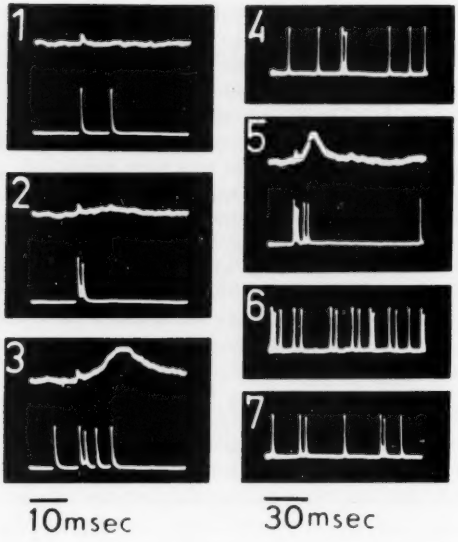


Fig. 27. Effect of adequate stimulation of muscle receptors on VSCT unit of E-type. Simultaneous recording from left dissected spinal half (except dorsal column) and VSCT fibre in left ventro-lateral funiculus (records 1—3 and 5). Records 1—3 on increasing stimulation of the right hamstring nerve. Record 4 shows the resting activity and record 5 the effect of supramaximal stimulation of the right hamstring nerve. Record 6 was obtained on strong pulling of the right quadriceps tendon and record 7 about 2 seconds after release of pulling. Unanaesthetized preparation.

ceps or triceps nerves, were tested for effects on adequate stimulation of receptors in the quadriceps and triceps muscles.

The I-units were regularly inhibited on stretch or contraction of the quadriceps and triceps muscles of the contralateral hindlimb. The inhibition usually appeared on very slight stretch or contraction, but could sometimes be evoked only on strong stimulation. Pinching of or pressure against the muscle or tendon also evoked inhibition. This was often marked already on very slight pressure. Sometimes units were found which were only slightly inhibited on stretch or contraction but nevertheless strongly inhibited on pressure. The effects mediated by the

quadriceps nerve were found not only on pressure of the muscle and quadriceps tendon, but also on pressure of the patellar tendon.

The E-units expectedly showed quite a different behaviour. The same manipulations that caused inhibition of the I-units led to acceleration of the E-units. Fig. 27 shows an E-unit which was activated from Ib afferents in the hamstring but not in the quadriceps nerve. Record 1 shows the "Ib spike" in the unit which is followed by further spikes on increased stimulation (records 2 and 3). Record 4 shows the resting activity of about 60 impulses per second and in record 5 the hamstring nerve is stimulated supramaximally. This results in the early burst of spike-activity which is followed by the typical late pause (cf. Fig. 25, p. 67). Stretch of the quadriceps muscle resulted in acceleration of the resting discharge to a frequency of about 150 impulses per second (record 6). Record 7 was obtained about two seconds after the release of the stretch and shows that the resting activity has reappeared. A similar though slightly less marked acceleration was obtained on stretch of the triceps muscle.

In two experiments the quadriceps and triceps muscles were prepared bilaterally in order to assess the effects not only from contralateral but also from ipsilateral muscles. The effects were tested on VSCT units monosynaptically activated from the right hamstring nerve. 10 units of I-type were encountered. The results are summarized in Table 4. As usual inhibition was obtained from the right (contralateral) muscles except for one unit (nr 6) which accelerated on stretch of the triceps muscle. This unit was also exceptional in that it accelerated more on supramaximal tetanic stimulation than on group I tetanization of the hamstring nerve. In this case probably the late excitatory action, which follows the inhibitory one on single shock stimulation, dominated. As shown in the table, stretch of the left (ipsilateral) muscles in most cases gave weaker effects than stretch of the right ones. One of the units (nr 8) was not influenced from either of the two left muscles, and three (nrs 3, 4, 7) were only influenced from one of them. The other units received either excitatory or inhibitory effects. In two units the excitatory

TABLE 4

Nr.	Resting frequency	Right		Left	
		Q	GS	Q	GS
1	0	−−	−−	+	+
2	3	−−	−−	++	+
3	10	−−	−	0	+
4	6	−−	−−	−	0
5	10	−−	−−	++	−
6	5	−−	+	−	−
7	5	−−	−	−	0
8	0	−−	−−	0	0
9	0	−−	−−	++	++
10	15	−−	−−	++	+

Effects on stretch of right and left quadriceps (Q) and gastrocnemius-soleus (GS) muscles on VSCT units discharged from Ib afferents in right hamstring nerve (two experiments). All units of I-type. Inhibition indicated with —, and facilitation with +. Double signs indicate strong effects.

effects were rather strong (nrs 9 and 10). In unit nr 9 these effects were displayed as a discharge in the otherwise silent unit and in nr 10 as a marked acceleration of the resting discharge. The effects obtained from the ipsilateral muscles are to be expected from the previous experiments with electrical stimulation of severed nerves and should be compared with the effects on adequate stimulation of cutaneous receptors (see below).

The inhibition or acceleration was most intense during the first few seconds of adequate stimulation but weaker effects usually remained as long as the stimulation continued. The I-units were usually completely silenced for two to five seconds. Then a spiking activity ensued with a much lower frequency than under resting conditions. This slow activity seldom showed any signs of further adaptation. After release of stimulation the resting activity sometimes reappeared abruptly but there was often a continuation of the increased or decreased activity during several seconds. In other cases release of stimulation was followed by a marked rebound in the I-units and a depression in the E-units.

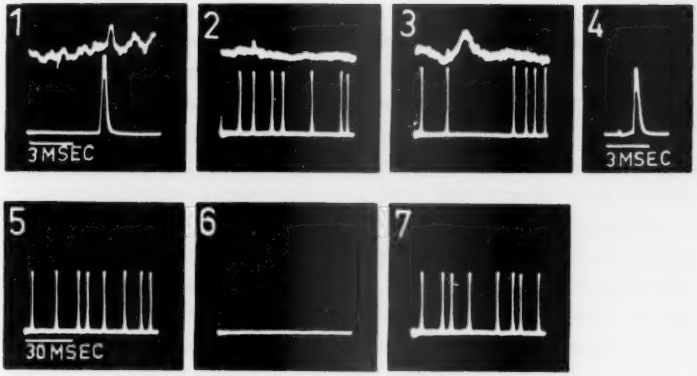


Fig. 28. Effect of adequate stimulation of muscle receptors on VSCT unit of I-type. Simultaneous recording from left dissected spinal half (except dorsal column) and from VSCT fibre in left ventro-lateral funiculus (records 1—3). Record 1 on maximal group I stimulation of the right triceps nerve. Record 2 on submaximal group I and record 3 on supramaximal stimulation of this nerve. Record 4 shows the antidromic spike appearing on stimulation of the dissected spinal half. Record 5 shows the resting activity in the unit. Record 6 obtained on slight pulling of the right triceps muscle and record 7 about 2 seconds after release of pulling. Records 2, 3 and 5—7 with the same sweep speed. Unanaesthetized preparation.

B. *Effects from muscles with strong Ib connection to the investigated neuron*

The inhibition of I-units and excitation of E-units from muscles not supplying the respective VSCT units with strong excitatory Ib action was expected from the findings on electrical stimulation of severed nerves. The next step was to investigate the effect of stretch and contraction of muscles with strong monosynaptic Ib connection to the investigated VSCT neurons. It was a surprise to find that this effect was exactly the same as that obtained from muscles without such connection. Fig. 28 illustrates a unit of I-type, monosynaptically activated from group I afferents in the triceps nerve. Records 1—4 are shown for identification of the unit. Record 1 shows the latency of the Ib spike on a fast sweep. In record 2 the triceps nerve was stimulated to give the Ib spike in the VSCT unit and also a distinct

VSCT mass discharge. The stimulus strength was, however, not strong enough to excite the efferent fibres and no appreciable contraction of the muscle was noted. The resting discharge in the unit is consequently uninfluenced. In record 3 the nerve is stimulated supramaximally with the result of a long pause in the discharge. The muscle contracted isotonically, when the record was photographed, but a similar pause was obtained on isometric contraction. Record 4 shows the antidromic spike appearing on stimulation of the dissected spinal half. The resting discharge is shown in record 5. The triceps tendon was strongly pulled by hand when record 6 was taken. This silenced the unit completely. Record 7, obtained a few seconds after release of the pull, shows that the basic discharge has reappeared. A similar inhibition was regularly found on adequate stimulation of muscles with Ib connection to the VSCT neurons. Thus it was also found when the connection was very strong as shown by the fact that the secondary neuron followed stimulation frequencies up to more than 500 per second for a period of several seconds.

The experiments with adequate stimulation showed that the I-units, when influenced by the discharge in the muscle afferents on stretch or contraction, were inhibited and not excited. Under these conditions evidently the inhibitory effects from the high threshold afferents dominate and conceal the monosynaptic excitatory action from Golgi tendon organ afferents. In the E-units acceleration was found already from muscles not supplying the units with Ib afferents, and the effects from muscles with Ib connections were similar. No appreciable difference was found in the effectiveness of accelerating the resting discharge between muscles supplying, and muscles not supplying, the unit with monosynaptic Ib excitation. Naturally Ib effects must add to the excitatory action from high threshold afferents, but such an addition is certainly very difficult to display.

The experiments described above suggest that the monosynaptic Ib connection to VSCT neurons is of little, or no, functional significance. In order to obtain more definite proof for this assumption, experiments were arranged in which the conditions for stimulation of Golgi tendon organs were as favourable as

possible. The triceps nerve was left in connection with its muscle and the tendon of this was freed and could be attached to an isometric myograph. The L VII and S I ventral roots were severed and the peripheral ends were placed on stimulating electrodes. The triceps nerve could be stimulated with another pair of electrodes. VSCT units activated from Ib afferents in the triceps nerve were examined on isometric contraction of the muscle caused by tetanic stimulation of the L VII and S I ventral roots. Strong isometric contraction is known to be a most effective stimulus for Golgi tendon organ afferents (MATTHEWS 1933, HUNT 1954, cf. also GRANIT 1950, 1952, HUNT 1952, LUNDBERG and OSCARSSON 1956) and should result in a discharge in the muscle afferents containing a maximal proportion of impulses in Golgi tendon organ afferents.

Five experiments were performed and 21 VSCT units encountered. 2 of these were E-units and accelerated during contraction. The 19 I-units could all be inhibited on stretch of the triceps muscle. This was shown either as cessation of a resting discharge or as inhibition of a labile test-spike evoked by a weak single shock stimulation of the triceps nerve. Most of the units were lost because of the movement ensuing on isometric contraction, but 8 of them could be examined in detail. In no case did isometric or isotonic contraction caused by tetanic stimulation of the ventral roots result in a discharge in the VSCT units, and units with a resting activity were silenced. These results were obtained on weak and strong, up to maximal, isometric or isotonic contraction.

The effects of isometric contraction were also tested as illustrated in Fig. 29. Identification of the unit was obtained from the Ib spike appearing on group I stimulation of the triceps nerve (record 1). The strength of the Ib connection was judged by the maximal stimulation frequency which the unit could follow. The unit shown in the figure had not a very strong connection, as it followed to a frequency of about 150 per second and that only initially (record 2). Record 3 shows stimulation of the triceps nerve with a slightly submaximal group I volley. The tendon is not attached to the strain gauge and the uppermost beam indicates zero tension. The tendon was

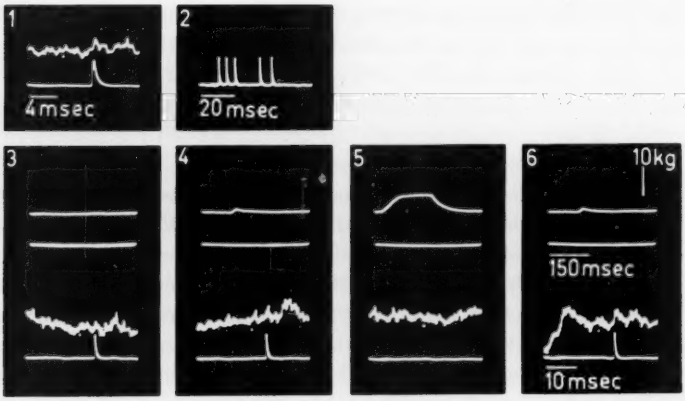


Fig. 29. Inhibition of VSCT unit of I-type on isometric contraction of the muscle supplying the unit with excitatory Ib action. Record 1, obtained on maximal group I stimulation of the right triceps nerve, shows simultaneous recording from left dissected spinal half (except dorsal column) and VSCT fibre in left ventro-lateral funiculus. Record 2 obtained on tetanic group I stimulation of the right triceps nerve. Records 3—6 show, from above downwards, strain gauge recording, reference line for myogram, recording from dissected spinal half, and recording from the VSCT unit. Record 3 obtained on weak stimulation of the right triceps nerve, the Achilles tendon not being attached to the strain gauge (zero level). The stimulation of the triceps nerve was unchanged in records 4—6 but the tendon attached to the strain gauge at a tension of about 400 grams. Record 5 was obtained on conditioning with maximal isometric contraction of the triceps muscle caused by tetanic stimulation of the severed S I+L VII ventral roots. Unanaesthetized preparation.

then connected to the strain gauge at a resting tension of about 400 grams and record 4 taken. The contraction of the muscle causes a small hump in the myogram. In record 5 the test shock to the triceps nerve was unchanged but its effect was conditioned by tetanic stimulation of the ventral roots causing a maximal contraction of the triceps muscle. The contraction results in inhibition of the test-spike. Record 6 was then taken without conditioning to ascertain if the micro-electrode remained in the fibre.

In all the 8 examined units the test-spike was inhibited when

due to a weak or moderate stimulation of the triceps nerve. The inhibitory effects appeared already with a weak contraction and increased with increasing strength of contraction. Some of the units had very strong Ib connections in that they followed frequencies up to 450 per second. In some units the test-spike was inhibited even when evoked by a maximal group I volley from the triceps nerve. This was the case in one of the units which followed to a frequency of 450 per second and illustrates how very effective the inhibition may be. Even the most effective adequate activation of Golgi tendon organs can not be expected to cause by far such a strong excitatory action as the synchronous volley evoked by single shock stimulation.

The ineffectiveness of the Ib afferents in discharging the VSCT neurons of I-type on adequate stimulation is probably largely due to a comparatively weak synaptic articulation. In Chapter II the Ib connection with VSCT neurons was shown to be more susceptible to asphyxia and anaesthesia than the group I connection with DSCT neurons. The "early discharge", which appears in the primary afferents from muscle spindles and Golgi tendon organs on single shock stimulation of muscle nerves in connection with their muscles (HUNT and KUFFLER 1951), is often transmitted to the DSCT neurons and appears as a burst of post-synaptic spikes (LAPORTE and LUNDBERG 1956, LUNDBERG and OSCARSSON 1956). Such a post-synaptic "early discharge" was not observed in the VSCT neurons suggesting that the synaptic articulation between the Ib afferents and the VSCT neurons is too weak to permit transmission of the somewhat dispersed impulses constituting the "early discharge".

The "early discharge" has been demonstrated also in group II fibres (HUNT 1954) and the possibility that it appears in group III fibres cannot be excluded at present. This discharge may add to the inhibitory effects on contraction but the good consistency between the effects on contraction and passive stretch do not suggest that this factor is of any major importance.

C. *Units with aberrant behaviour*

In the 11 later experiments, with an improved technique of testing and in which all units were carefully examined, 150

VSCT units were encountered, 80 of which were discharged from Ib afferents in the muscles used for adequate stimulation. All these units behaved in accordance with the pattern described above except for the unit already discussed as nr 6 in Table 4 and 6 other units to be described presently.

Three units with Ib connection to the quadriceps nerve and responding with further spikes on stimulation supramaximal to group I, expectedly accelerated on stretch of the quadriceps muscle. These units, however, deccelerated on stretch of the semitendinosus muscle and one of them also on stretch of the triceps muscle. The other two units accelerated on stretch of the latter. These units thus behaved as E-units in connection with some muscles and as I-units in connection with others.

Two units monosynaptically activated from the quadriceps nerve and one from the triceps nerve belonged to the E-type according to definition but were nevertheless inhibited on stretch of all the muscles. These units responded with only one or two further spikes on stimulation supramaximal to group I. These spikes were suppressed on very slight stretch of the muscle. Probably in these units the inhibitory action, which follows the excitatory one in E-units, dominated on adequate stimulation.

Comments

The experiments reported in this section were concerned with the effects of adequate stimulation of muscle receptors on VSCT neurons. In no case were any appreciable effects attributable to Golgi tendon organ afferents observed, despite that some of the experiments were specially designed to provoke strong stimulation of the Golgi tendon organs. However, strong effects were consistently obtained on stretch and contraction of the muscle and on pressure against the muscle or tendon. These effects were indistinguishable from muscles supplying, and muscles not supplying, the investigated neuron with excitatory Ib action and conform to those to be expected from high threshold muscle nerve afferents according to the previously reported experiments with electrical stimulation of severed nerves. This indicates that the VSCT neurons, on adequate stimulation of muscle receptors,

are dominated by the effects from high threshold muscle nerve afferents, and suggests that the monosynaptic connection with Golgi tendon organ afferents is of little, or no, functional significance.

2. Adequate stimulation of cutaneous receptors

Electrical stimulation of skin nerves influences the VSCT mass discharge perhaps even more than supramaximal stimulation of muscle nerves (cf. Chapter IV). The effects are very similar to those obtained on stimulation of high threshold muscle nerve afferents. In this section will be shown that the VSCT neurons receive very strong effects from skin receptors on adequate stimulation and that the receptive field is extensive.

METHODS. Cats under nembutal anaesthesia or unanaesthetized decerebrate cats were used. The animals were spinalized at the upper thoracic region. The VSCT mass discharged was recorded from the dissected left half of the spinal cord and VSCT units were recorded in the left lateral funiculus at the L I region. The VSCT neurons were identified as units monosynaptically connected to group I afferents in the right hamstring and, in some experiments, also the right quadriceps nerve. Both hindlimbs were denervated except for the saphenus, cutaneous peroneal, sural, and lateral cutaneous nerve passing through the biceps muscle. The latter skin nerve (cf. LANGLEY and HASHIMOTO 1917) was constantly found and often as large as the sural nerve.

The hair was cut short on both hindlimbs and the cutaneous receptors stimulated by bending of hairs, stroking against the hair with a blunt object, pressure, and pinching.

In unanaesthetized animals it was found difficult to keep the units due to reflex movements and therefore the first experiments were performed on anaesthetized ones. In six experiments 47 units, monosynaptically discharged from group I afferents in the hamstring nerve, were carefully investigated for effects on adequate stimulation of cutaneous receptors. As most of the VSCT units are silent in the anaesthetized animal, the effects were usually tested on the labile spike caused by a carefully adjusted stimulus to the right hamstring nerve. The encountered units have been arranged in ten groups in Fig. 30 and will be discussed in relation to this figure.

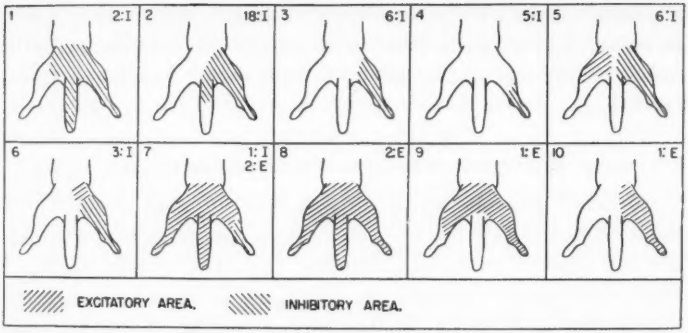


Fig. 30. Effects on adequate stimulation of skin receptors in cats under nembutal anaesthesia. Analysis of 47 VSCT units (6 experiments) which could be monosynaptically discharged from Ib afferents in the right hamstring nerve. Approximative areas from which inhibitory and excitatory effects could be evoked on adequate stimulation indicated by hatching. Units divided into 10 groups denoted 1, 2, 3 . . . in upper left corner. Number and type (I- or E-type) of encountered units indicated in upper right corner.

All the I-units were characterized by inhibition from the right hindlimb. Most of the units could be inhibited from the whole skin area of the right hindlimb (groups 1, 2, and 5) and some units also from the proximal part of the left hindlimb and from the tail (group 1). In a few units the inhibition was restricted to the distral part of the right hindlimb (groups 4 and 7). Some of the units received facilitation from small skin areas. This facilitation was obtained from the upper part of the left thigh (group 5) or from the lateral and most proximal part of the right thigh (group 6). The areas shown in the figure are approximative and some units deviated slightly from the shown pattern.

The inhibitory effects were evoked by pinching of the skin. Touch did not influence the units in most cases despite that many were inhibited already at very slight pinching. However, in a few cases slight inhibitory action was obtained on touch or slight pressure. The facilitation could be evoked only on pinching in five units but in five slight effects were obtained also on touch.

The E-units behaved quite differently. Of the six units encountered two received strong excitatory action from both hindlimbs (group 8) and two rather strong effects except from the distal part of the right leg (group 7). The last two units had somewhat smaller excitatory areas (groups 9 and 10). Of special interest are the units collected as group 7. Two of these were of E-type whereas the third was of I-type. These units behaved similarly and seem to constitute transitional links between the E- and I-units. One of these E-units is shown in Fig. 31. The upper beam shows recording from the dissected spinal half and the lower one from the VSCT unit. Records 1—8 are shown for identification. Record 1 was obtained under resting conditions but in records 2—5 the right hamstring nerve was stimulated with increasing strength. The "Ib spike" appears already with a submaximal group I volley as shown in record 2. In record 4, with the stimulus strength increased to include high threshold afferents, further spikes appear showing that the unit is of E-type. On supramaximal stimulation three or four late spikes appear (record 5). Records 6 and 7 were obtained with a slower sweep speed. In record 6 group I stimulation results in the "Ib spike" but otherwise the resting discharge is uninfluenced. On supramaximal stimulation the short burst of spikes evoked from high threshold afferents is followed by a pause with a duration of about 90 msec. A similar pause was obtained on supramaximal stimulation of the left hamstring nerve from which no excitatory action was evident (record 8). The unit had a resting discharge of about 30 impulses per second (record 9). Record 10 was taken during slight pinching of the skin of the posterior surface of the right foot which completely silenced the neuron. No certain effects were obtained from the inhibitory area on touch or stroking. The skin was slightly pinched at the left side over the sacrum when record 11 was taken. The discharge increased to about 75 per second. A similar acceleration could also be obtained by pinching of other parts of the excitatory area. Touch or stroking gave hardly appreciable effects from most parts of this area with the intense resting activity as background. Such effects could, however, be displayed by decreasing the resting discharge

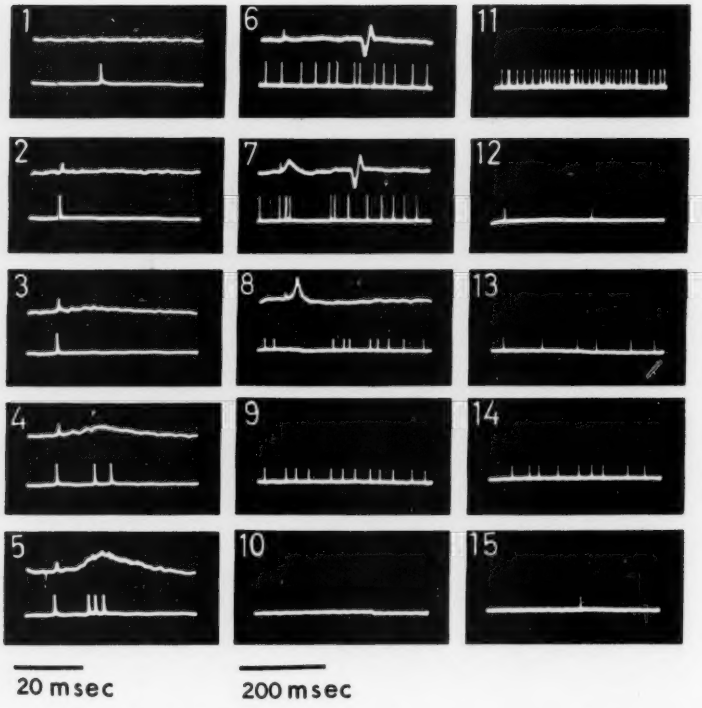


Fig. 31. Effects of adequate stimulation of skin receptors on VSCT unit of E-type belonging to group 7 in the scheme of Fig. 30. Simultaneous recording from left dissected spinal half (except dorsal column) and from VSCT fibre in left ventro-lateral funiculus (records 1—8). Mass discharge recording distorted by electrocardiogram in records 6 and 7. Records 2—5 obtained on increasing stimulation of the right hamstring nerve. Record 6 on slightly submaximal group I and record 7 on supramaximal stimulation of the right hamstring nerve. Record 8 on supramaximal stimulation of the left hamstring nerve. Record 9 shows the resting activity in the unit. Record 10 obtained on slight pinching of the skin of the posterior surface of the right foot and record 11 on slight pinching of the skin over the sacrum on the left side. Records 12—15 obtained on very slight pinching of the skin on the right foot. In addition the skin was slightly stroked against the hairs on the lateral and proximal part of the left thigh when records 13 and 14 were obtained. Nembutal anaesthesia.

through slight pinching of the skin of the right foot. This was done when records 12—15 were obtained. During the two middle records (13, 14) the skin was stroked against the hairs which resulted in a marked acceleration. The effects on stroking were especially easy to evoke at the lateral and most proximal parts of the thighs bilaterally. It is of interest to note that in spite of the inhibitory action obtained from high threshold muscle nerve afferents from the left side, excitation was obtained on adequate stimulation of skin receptors.

Of the other two units belonging to group 7 the other E-unit was similar to that shown in Fig. 31. The I-unit differed in that it was silent and more difficult to excite on touch. Pinching within the excitatory area led to a discharge of the unit.

The E-units in groups 8—10, Fig. 30, had all a resting discharge which varied from about 10 per second (the units in groups 9 and 10) to between 30 and 40 per second. Acceleration was obtained on pinching, but slight excitatory effects were also evoked on touch or stroking.

The results on unanaesthetized cats were in accordance with the findings on anaesthetized ones. The effects from the skin receptors were, however, much stronger and richer in details. Four experiments were performed and 15 units monosynaptically discharged from group I afferents in the right hamstring nerve were thoroughly examined. All of them were I-units. As the I-units encountered in the anaesthetized cats, these were characterized by strong inhibitory effects from the right hindlimb. According to the extension of the inhibitory area, these units could be arranged into the groups of the scheme shown in Fig. 30. The distribution of units to the different groups corresponded well to that found in the previous experiments. Thus most of the units belonged to group 2. The inhibitory effects were very strong and could usually be obtained on very slight touch. Most of the units were spontaneously active and the inhibition was displayed as a decrease or cessation of the resting discharge. Many of the units were completely silenced already on bending of one or a few hairs. A striking difference from the conditions in the anaesthetized preparation was that all the units were influenced also from the left (ipsilateral) side. The

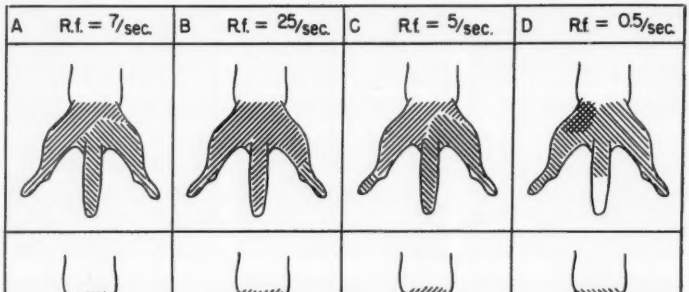


Fig. 32. Effects of adequate stimulation of skin receptors in unanaesthetized preparations on 4 VSCT units which could be monosynaptically discharged from Ib afferents in the right hamstring nerve. Upper row, dorsal view; lower row, ventral view. R. f. = resting frequency.

effects from this side were often weaker than those from the right, but in some units as strong. Usually excitatory action was obtained from the ipsilateral side and that was the case in 11 of the 15 units. The excitatory effects were evoked on slight touch.

The excitatory area usually encircles the inhibitory one as shown in Fig. 32: A. The illustrated unit corresponds to group 2 in the scheme of Fig. 30. Acceleration of the resting discharge was obtained on touch from the whole excitatory area but was most marked from the right side. B shows another unit which was inhibited only from the right foot, the rest of the receptor area giving acceleration. This unit corresponds to group 7, but evidently also to group 4, in the scheme. Two units which received excitatory action from the left hindlimb were nevertheless inhibited from the left foot area. One of these units is illustrated in Fig. 32: C.

4 of the 15 units showed inhibition and not facilitation from

the left side. The effects were definitely weaker from the left than from the right side. Usually, however, the effects were evoked already on touch or slight pressure. One of the units is shown in Fig. 32: D. Pinching resulted in inhibition from the whole left side up to the crest of the hip bone. Nevertheless slight touch within a small area of the lateral part of the thigh resulted in acceleration of the resting discharge. Such mixed effects have been observed in only two other VSCT units (cf. Fig. 33: D). Mostly the excitatory and inhibitory areas were sharply demarcated with either excitatory or inhibitory effects on touch, pressure, and pinching.

Manipulating the tail sometimes caused inhibition and sometimes excitation. Usually the effects were weak and only evoked on pinching, but in some cases, when the excitatory area was large and also included the proximal part of the right hindlimb, acceleration was obtained on slight touch.

The resting frequencies of the four units are marked out in the figure. The unit with the largest excitatory area has the highest frequency and the unit with the smallest area the lowest frequency. This correspondence between the frequency and the size of the excitatory area was observed in all the experiments and suggests that the resting discharge partly depends on impulses from cutaneous receptors.

In the experiments on not anaesthetized cats also the quadriceps nerve was stimulated during the search for VSCT units. In Chapter III it was shown that whereas one group of VSCT units receives excitatory Ib action from usually all the three hamstring nerves and the triceps nerve, another group is activated from the quadriceps and also often from the triceps nerve. It was of interest to determine if these two groups also differed in their connections with skin afferents. It was found that the "quadriceps units" were similar to the "hamstring units", but that there was some difference in the extension of the excitatory and inhibitory areas. The 10 encountered "quadriceps units", which all were of I-type, had large excitatory skin areas. Some of the units are illustrated in Fig. 33. The excitatory area often extended down to the knee or longer on the right hindlimb. 8 of the 10 units may be represented by A and B

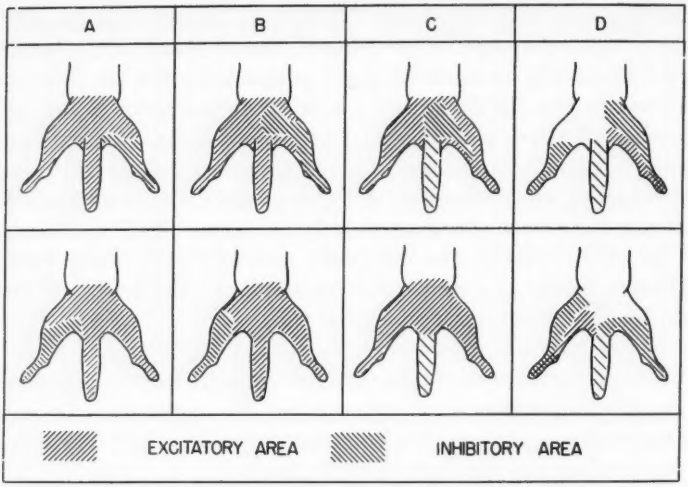


Fig. 33. Effects of adequate stimulation of skin receptors in unanaesthetized preparations on 4 VSCT units which could be monosynaptically discharged from Ib afferents in the right quadriceps nerve. Weak effects indicated by sparse hatching. Upper row, dorsal view; lower row, ventral view.

in Fig. 33. In A, representing 5 units, the excitatory skin flap covered approximately the quadriceps muscle and in B approximately the hamstring and adductor muscles.

The last two "quadriceps units" are shown in C and D. Both these units are unique among the encountered I-units in that the excitatory area extended down to the distal part of the right hindleg. C shows a unit with a very limited inhibitory area consisting of a zone on the proximal part of the right hindlimb. Fig. 33: D depicts a "quadriceps unit" with a somewhat aberrant behaviour. It was the only one which received inhibitory action from the left hindlimb. This inhibitory action was weak and no influence at all could be detected from the proximal part of the limb. Both excitatory and inhibitory effects were obtained from the right side as shown in the figure. Acceleration was evoked on slight touch of the right foot but pinching resulted in inhibition which was followed by excitatory rebound.

The large excitatory area found in the "quadriceps units"

should perhaps be correlated to the finding that E-units are found more often among the "quadriceps" than among the "hamstring units" (Chapter I). All evidence points to the I-units and E-units being only the extremes on a continuous scale of general behaviour. Previously several units intermediate between the two types have been described. The "quadriceps units" seem to be nearer to the end of the scale characterized by E-units than are the "hamstring units".

In the experiments with unanaesthetized preparations special attention was payed to adaptation of the skin effects. The adaptation was similar for the excitatory and inhibitory effects. The strong effects obtained on slight touch and especially those obtained on slight stroking against hairs were always very rapidly adaptating. Mostly the excitation showed up as a rapid burst of impulses, and the inhibition as a quick cessation of the resting activity. The effects on pressure and pinching had both slowly and rapidly adaptating components. The rapid component may, of course, be due to the same receptors as those causing the effects on touch. Slight pinching within the inhibitory area often resulted in complete inhibition during some seconds whereafter a slow activity began. Sometimes this activity soon reached the resting level but in other cases the discharge continued with a low frequency as long as the stimulation continued.

When the stimulation ceased, the resting activity usually returned almost at once. In many cases, however, there was a definite after-effect of sometimes considerable length. In a few cases inhibition of the resting discharge lasted for 5—10 seconds after cessation of pinching within the inhibitory area. The pinching was probably too weak to cause damage of the tissues, but it cannot be definitely excluded that the after-effects were due to a continuation of impulses from the stimulated area. In some cases release of stimulation was followed by a marked rebound.

Effects in the dorsal spino-cerebellar tract. In some experiments also DSCT units were recorded. These were identified as being monosynaptically activated by group I afferents in the ipsilateral hamstring nerve. 25 units in anaesthetized and 23 units in not anaesthetized prepara-

tions were investigated. The units in the anaesthetized animals were not appreciably influenced on touch or pinching. Touch did not influence the units in the not anaesthetized animals, and in 21 of the 23 units also pinching was ineffective. In one unit there was probably a slight inhibitory effect and in another a definite excitatory one. In the latter two units the effects appeared when pinching led to reflex movements of undenervated hip muscles and were probably due to a discharge in afferents from these muscles. It is concluded that the DSCT neurons are, as a rule, not influenced on adequate stimulation of skin receptors.

Comments

The experiments reported in this section were concerned with the effects of adequate stimulation of skin receptors on VSCT neurons. The results were in good accordance with the previously reported experiments with electrical stimulation of severed nerves. The extensive spatial convergence to be expected from these experiments was confirmed in that skin effects could be evoked, as a rule, from both hindlimbs, the tail, and the skin covering the pelvic girdle. The effects on electrical stimulation of skin nerves were very strong and, in confirmation, the effects on adequate stimulation usually appeared already on very slight tactile stimulation.

3. Adequate stimulation of receptors in deep structures

Electrical stimulation of high threshold joint nerve afferents influences the VSCT neurons in a similar way as stimulation of high threshold muscle nerve afferents and low and high threshold skin nerve afferents. Consequently, it was of interest to investigate the effects of adequate stimulation of joint receptors. The hindlimbs were denervated except for the posterior knee joint nerve and units monosynaptically discharged from group I afferents in the contralateral hamstring nerve were examined. Unfortunately no definite conclusion could be reached as unavoidable small movements transferred to undenervated skin and muscles of the pelvic girdle on movements in the knee joint, strongly influenced the VSCT neurons.

However, some observations on units encountered in the experiments described above may have relevance to this problem.

In many units in the anaesthetized cats the inhibitory effects on pinching of the skin of the right foot were rather weak. In spite of this it was regularly found that extension or flexion of the toes resulted in a marked inhibition. The effects were most marked on strong bending of the toes and may have been caused by activation of pain afferents. In many cases inhibition was evident already on small movements and could hardly have been due to nociceptive stimulation. Similar effects were also obtained from the left foot in the experiments with unanaesthetized animals. In these cases the effect was acceleration except when the skin of this area gave inhibition. The joint effects were rapidly adaptating except when strong and presumedly nociceptive stimulation was used.

The results obtained on electrical stimulation of severed nerves indicated that the joint nerve effects were due to high threshold afferents. The specific joint receptors are known to be connected to the low threshold afferents (SKOGLUND 1956) which do not appreciably influence the VSCT neurons. Probably the effects described above are due to stimulation of other types of receptors, perhaps mainly localized to ligaments and periosteum. This assumption receives some support from the finding that, when only weak effects were obtained from the skin, pressure against deep structures sometimes resulted in inhibition or excitation.

4. Effects displayed on mass discharge recording

The results reported in the previous sections were obtained on recording from single units. The strong effects from high threshold muscle nerve afferents and skin afferents on adequate stimulation suggest that some of the more general effects might be shown on mass discharge recording. This was confirmed in that the VSCT mass discharge evoked on muscle nerve stimulation was much reduced on stretch of the same or other muscles. Fig. 34 shows the effect of stretch of the quadriceps muscle on the VSCT discharge evoked on group I stimulation of the hamstring nerve. Initially the mass discharge was reduced to between 10 and 20 per cent of the unconditioned value. As about 10 per cent of the VSCT units, the E-units, on stretch are facili-

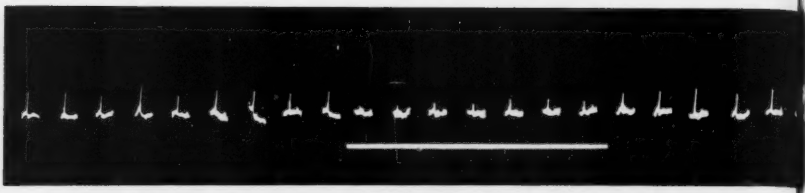


Fig. 34. Effect of stretch of muscle on VSCT mass discharge. Recording of the VSCT mass discharge from the left dissected spinal half (except dorsal column) on maximal group I stimulation of the right hamstring nerve. White line indicates strong pulling by hand of the right quadriceps tendon. Records obtained on running film with intervals of one second. Electron beam unconventionally traversing from right to left.

tated and not inhibited, this indicates that almost all the I-units were prevented from discharging.

Somewhat weaker effects were obtained on adequate stimulation of skin receptors. The VSCT mass discharge evoked on hamstring nerve stimulation diminshed on pinching of the skin of the contralateral hindlimb. The effects were most marked from the foot and the lower part of the leg but could usually be displayed also from the thigh and from the skin over the sacrum at the contralateral side. No certain effects could be obtained from the ipsilateral hindlimb. There was maximally a reduction to 50—60 per cent of the unconditioned value. Thus the inhibition was not as marked as on stretch of muscles but the effect must nevertheless be considered as very strong as it was evoked from a very small part of the receptive field.

DISCUSSION

Adequate stimulation of receptors in contralateral muscles without strong Ib connection to the investigated VSCT neurons caused inhibition of I-units and excitation of E-units (for definition of I- and E-units see Chapter I). Weaker effects were obtained from ipsilateral muscles which provoke either excitation or inhibition in the I-unts. The effects appeared on stretch or contraction of the muscle and on pressure against the muscle

or tendon. It has previously been shown that the inhibition appearing on electrical stimulation supramaximal to group I afferents, appears with activation of group II afferents but is mainly due to afferents of higher threshold. The inhibitory effects sometimes appearing on very slight stretch may thus be due to group II afferents which are connected with stretch receptors of a rather low threshold (HUNT 1954). However, the effects on strong stretch, almost completely abolishing the VSCT mass discharge, cannot be explained as due to activation of only group II afferents, but must partly be caused by activation of group III and perhaps also group IV (C-fibres) afferents. It is of interest that these fibres, the function of which is not known with certainty, apparently may be activated on stretch or contraction. The effects of pressure must at least partly be due to afferents of higher threshold than group II, as they could be evoked not only from muscles but also from tendons.

The effects from muscles not strongly connected to the VSCT neurons with Ib afferents were expected from findings on electrical stimulation of severed nerves. It was, however, very remarkable that adequate stimulation of muscles with strong Ib connection to the investigated neurons gave effects which were indistinguishable from those obtained from muscles without such connection. In 11 successful experiments 80 VSCT units were examined on adequate stimulation of muscles supplying the units with strong Ib excitatory action and in no instance were appreciable effects assignable to the Ib afferents observed. The Ib effect is usually excitatory. In the I-units the excitation to be expected from impulses in the Golgi tendon organ afferents was evidently concealed by the simultaneously impinging impulses from high threshold muscle nerve afferents. In E-units the effect of stretch or contraction was acceleration of the resting discharge even from muscles without strong Ib connection and, as far as could be judged, the effect was identical from muscles with such connection. In these units the excitatory action from the Ib afferents must somewhat increase the acceleration of the resting discharge, but this increase was too weak to be observed. Similarly the sometimes encountered inhibitory Ib effects must cause subsidiary inhibition of I-units. The Ib in-

hibition is weak and seldom encountered and can not be expected to affect the VSCT units appreciably.

The autogenetic inhibition of motoneurons (for a review see GRANIT 1955b) may be increased under certain experimental conditions. In spinalized cats inhibition may be marked if the muscle is cold and in a bad circulatory state (JOB 1953). In the present investigation the contingency of such effects was avoided in that precautions were taken not to damage the blood vessels to the muscle and in that the muscle was kept at a normal temperature with an electrical heater. Some experiments were performed on not spinalized decerebrate cats and no difference in the behaviour of the VSCT units was found from that in the spinalized preparations. Neither is there any reason why the VSCT units should be influenced as the motoneurons in this respect.

The experiments with the muscle contracting isometrically on tetanic stimulation of ventral roots are especially elucidative for the problem of the strength of the Ib effects in comparison with the effects from high threshold muscle nerve afferents. Isometric contraction is probably the most effective stimulus for Golgi tendon organs which are stretch receptors with a rather high threshold (MATTHEWS 1933, HUNT 1954, cf. also GRANIT 1950, 1952, LUNDBERG and OSCARSSON 1956). In no case did such a stimulation evoke a discharge in the I-units and when a resting activity existed this was inhibited. The effects on isometric contraction were also tested on a labile test-spike evoked by weak electrical stimulation of the muscle nerve. Regularly such a test-spike was inhibited by the conditioning contraction. In some cases a test-spike evoked even by a maximal group I volley in units with very strong Ib connection was inhibited during contraction. As the excitatory action exerted by a synchronous Ib volley must be much more effective in discharging the VSCT units than the dispersed impulses on adequate stimulation these experiments clearly display the strength of the inhibitory effects from high threshold afferents in relation to the excitatory Ib effects.

On the other hand strong effects were obtained on adequate stimulation of skin receptors as could be expected from the findings on electrical stimulation of severed nerves. The VSCT units were influenced from a very extensive skin area usually

including both hindlimbs, the tail, and the skin covering the pelvic girdle. The I-units were inhibited from part of the contralateral skin area but often excited from the ipsilateral, whereas the E-units received strong excitatory action from usually the whole area. As a rule the skin effects, as the muscle effects, were stronger from the contralateral side.

The inhibitory area of the I-units was often circumscribed by the excitatory one. It was often fairly small and, when large, strong effects were sometimes obtained from only part of it. These facts strongly suggest that the VSCT units of I-type forward their essential message to the cerebellum not in form of increased spike activity but as a decrease or cessation of the resting activity. The often extensive excitatory area of the I-units may serve to provide the units with the necessary excitatory background for displaying the inhibition. Thus, the I-units may forward information concerning both stimulus strength and localization of stimulus. The functional significance of the E-units is more difficult to interpret; possibly these units are concerned with the maintenance of an excitatory state of certain cells in the cerebellar cortex.

As a rule, the effects from the same skin area were the same on touch, pressure, and pinching. In this respect the organization is similar to that found for the excitatory and inhibitory skin areas of the motoneurons described by HAGBARTH (1952). However, the effects on the motoneurons were most easily evoked on pinching, tactile stimulation being much less effective, while the skin effects on the VSCT neurons were strong even on slight tactile stimulation. The latter should perhaps be correlated to the fact that the VSCT neurons have been shown to receive strong inhibition from low threshold skin nerve afferents on electrical stimulation of severed nerves. This inhibition increases further when the electrical stimulation is raised to include also high threshold afferents. However, a closer comparison between the results on electrical and adequate stimulation would hardly give any further information as there seems to be no strict correlation between different modalities of cutaneous sensation and different fibre sizes. Thus ZOTTERMAN (1939) showed that already slight touch may evoke a discharge

in both fast and slowly conducting cutaneous afferents (cf. also MARUHASHI, MIZUGUCHI, and TASAKI 1952).

The effects from skin receptors were very strong and suggest that the VSCT mainly is a pathway for exteroceptive information. The convergence of similar effects from high threshold muscle and joint nerve afferents is more difficult to interpret, but one possibility is that these afferents partly subserve an exteroceptive function. That receptors in deep structures may have such a low threshold that they probably are activated together with touch receptors of the skin on any "but the most trivial stimulus" was suggested by MOUNTCASTLE, COVIAN, and HARRISON (1950) from experiments on denuded isolated limbs. In the present experiments it was noted that slight pressure against deep structures, certainly too weak to be nociceptive, sometimes strongly influenced the VSCT neurons. These effects were further increased on stronger, probably nociceptive, stimulation of the same structures.

The findings presented here raise the question why the most conspicuous feature of the VSCT on electrical stimulation of severed nerves, namely the monosynaptic connection with Golgi tendon organ afferents, does not seem to play any functional rôle. It is possible that this connection is vestigial in the cat. It has previously been suggested (OSCARSSON 1956) that some features of the VSCT may be explained from the fact that this tract is phylogenetically old. The VSCT is found already in the most primitive vertebrates, whereas the DSCT probably has developed concomitantly with the development of extremities and muscle spindles (LARSELL 1937, 1956, cf., however, also KAPPERS, HUBER, and CROSBY 1936). The DSCT is monosynaptically activated from muscle spindle and Golgi tendon organ afferents (LAPORTE et al. 1956 a, b, LUNDBERG and OSCARSSON 1956) and adequate stimulation of muscle receptors indicates that it is a pathway forwarding impulses from stretch receptors (LAPORTE and LUNDBERG 1956, LUNDBERG and OSCARSSON 1956). Adequate stimulation of skin receptors does not appreciably influence the DSCT neurons even in the not anaesthetized preparation. Possibly the VSCT, earlier during the phylogenesis, was mainly concerned with forwarding in-

formation from stretch receptors. When the DSCT evolved, this took over the proprioceptive function and developed the pattern of reciprocal innervation well adapted to the complicated function of the muscles of the extremities. The ventral tract with its diffuse pattern of convergence of stretch afferents from different muscle nerves lost its importance as a pathway for impulses from stretch receptors and evolved into a pathway forwarding exteroceptive information.

SUMMARY

The effects of adequate stimulation of muscle and skin receptors on VSCT neurons were investigated.

Adequate stimulation of receptors in contralateral muscles results in inhibition of the VSCT neurons of I-type and in excitation of the VSCT neurons of E-type. Weaker and more varying effects are obtained from ipsilateral muscles. The effects are evoked on stretch and contraction of the muscle and pressure against the muscle or tendon. The effects from muscles with Ib connection to the investigated neuron and from muscles without such connection are indistinguishable. It is concluded that the monosynaptic connection between Golgi tendon organ afferents and VSCT neurons is of little, or no, functional significance. It is suggested that this connection is vestigial in the cat.

The VSCT neurons receive excitatory and inhibitory effects from cutaneous receptors of a large receptive field usually including the skin of both hindlimbs, the tail, and the skin covering the pelvic girdle. As a rule the effects are most marked from the contralateral side. The I-units are inhibited from the contralateral hindlimb or from part of it. In addition the I-units usually receive excitatory action from the ipsilateral limb and from the proximal part of the contralateral one. The E-units usually receive excitatory effects from the whole receptive field. The skin effects are evoked on slight touch, strong effects often being obtained on bending of a few hairs. Pinching results in stronger but similar effects.

It is suggested that the VSCT is a pathway mainly for exteroceptive information and that the essential message in the I-units is coded as inhibition of the resting discharge.

Comments

It is of interest to compare the functional organization of the dorsal and ventral spino-cerebellar tract. At present, these tracts are the only ascending spinal pathways which have been analysed in detail. They both connect the caudal part of the spinal cord with the cerebellar cortex, mainly that of the anterior lobe, and have conduction velocities ranging among the highest found in the nervous system.

Electro-physiological investigations indicate that the two tracts have different functions although there are similarities in the pattern of primary afferent connections to them.

Both tracts receive monosynaptic excitatory action from group I muscle nerve afferents. The DSCT has two subgroups, one connected with muscle spindle afferents and the other with Golgi tendon organ afferents (LUNDBERG and OSCARSSON 1956). With both these subgroups convergence is very restricted. The majority of neurons are supplied with monosynaptic excitatory action only from one muscle (HOLMQVIST et al. 1956). The VSCT neurons, on the other hand, are monosynaptically connected with only Golgi tendon organ afferents, and characterized by a widespread convergence from a number of muscles (Chapter III). Both tracts receive inhibitory action from group I afferents. In DSCT neurons this action is powerful and exerted from a rather wide receptive field although the reciprocal action dominates (LAPORTE et al. 1956 b, HOLMQVIST et al. 1956). In the VSCT inhibitory action caused by Golgi tendon organ afferents is encountered, but is usually weak.

Remarkable differences in function of the two tracts are perhaps best illustrated by experiments with adequate stimulation. The DSCT units behave as would be expected from their connections with muscle spindle and Golgi tendon organ afferents (LAPORTE and LUNDBERG 1956, LUNDBERG and OSCARS-

SON 1956). With the VSCT it has, despite the most stringent tests (Chapter V), not been possible to demonstrate that the synaptic actions from Golgi tendon organ afferents are of functional importance. This is presumably due to the relatively weak synaptic coupling between the primary afferents and the tract neurons; probably this connection is vestigial in the cat. On the other hand, very strong effects are obtained in the VSCT on electrical stimulation of high threshold muscle nerve afferents and on manipulation of muscles presumably leading to activation of these afferents. Strong effects are also evoked from skin and joint nerve afferents. With adequate stimulation particularly strong effects are evoked on stimulation of cutaneous receptors indicating that the VSCT may be a pathway forwarding exteroceptive information. The effects from high threshold muscle and joint nerve afferents are more difficult to interpret but possibly these actions are subsidiary to those from the skin afferents.

There is evidence that this combination of skin nerve and high threshold muscle and joint nerve afferents are not entirely without effect on the DSCT. HOLMQVIST et al. (1956) noticed that repetitive stimulation of ipsilateral skin nerves often influenced the DSCT neurons in either excitatory or inhibitory direction. In the present experiments it was found that a conditioning volley in a cutaneous nerve inhibited the mass discharge in the DSCT although to a much lesser degree than in the VSCT (page 60). Similar effects were evoked in the DSCT on supramaximal stimulation of muscle and joint nerves, and also in this case the effects were much weaker than in the VSCT. The inhibition had a similar time course in the two tracts. These findings may indicate that the VSCT and DSCT have a similar pattern of innervation in this respect, but it is obvious that there are great quantitative differences. Presumably the connections with skin nerve and high threshold muscle and joint nerve afferents are of little, or no, functional importance in the DSCT. It is noteworthy that the DSCT neurons even in the unanaesthetized animal were not influenced on adequate stimulation of cutaneous receptors (page 91). Neither does it seem likely that the DSCT neurons in any marked degree are influenced on adequate sti-

mulation of joint and high threshold muscle nerve afferents. This assumption receives some support from the finding that in the DSCT neurons the excitatory and inhibitory actions evoked by stretch or contraction are such that would be expected solely from the connections with muscle spindle and Golgi tendon organs (LAPORTE and LUNDBERG 1956, LUNDBERG and OSCARSSON 1956).

To summarize, there are indications that the DSCT and VSCT neurons have their connections with primary afferents organized according to basically similar patterns, but that great quantitative differences exist. All available evidence indicates that the DSCT is a pathway transmitting exclusively proprioceptive information, whereas the VSCT probably forwards exteroceptive information.

Whereas the proprioceptive information forwarded by the DSCT fits well with classical concepts concerning the cerebellum as a regulator of motor functions, nothing is known about the importance for the cerebellar functioning of the exteroceptive messages conveyed by the VSCT and other pathways. These messages may be of importance for the regulation of motor mechanisms (cf. HERRICK 1947) but they may also have to do with other possible functions of the cerebellum. Thus SNIDER (1950) and WHITESIDE and SNIDER (1953) suggested that the cerebellum might have a regulatory action also in the sensory sphere. A solution of the exact significance of the messages forwarded by the VSCT units probably has to await studies on single cells in the cerebellar cortex. The assessment of the conduction velocities of the spino-cerebellar tracts and the finding that the DSCT is uncrossed whereas the VSCT is crossed (OSCARSSON 1956) open new possibilities to investigate the synaptic connections between fibres of these tracts and neurons in the cerebellar cortex. Together with the knowledge of the behaviour of the tract units on adequate stimulation such investigations can be expected not only to give clues to the significance of the functional organization of the spino-cerebellar tracts, but also to give important information concerning the functioning of elements in the cerebellar cortex.

General Summary

This investigation has been concerned with the functional organization of the ventral spino-cerebellar tract (VSCT) in the cat. The results are described in five chapters, each ending with a discussion and a short summary.

VSCT neurons receive monosynaptic excitatory action from contralateral Golgi tendon organ afferents (Ib afferents), but no effects from group I muscle spindle afferents. The impulse transmission from Ib afferents to VSCT neurons shows several similarities with the impulse transmission from group I afferents to dorsal spino-cerebellar tract (DSCT) neurons, but is more susceptible to asphyxia and anaesthesia. VSCT neurons sometimes receive inhibitory action from Ib afferents. The convergence of effects from Ib afferents in various muscle nerves onto single VSCT neurons is rather diffuse and mainly excitatory. No appreciable group I effects converge onto the VSCT neurons from ipsilateral muscle nerves.

VSCT units receive strong effects from skin nerve afferents and high threshold muscle and joint nerve afferents. Two types of VSCT units are distinguished and denoted as I- and E-units. The I-units are the most numerous. In these units inhibitory effects dominate, whereas in the E-units excitatory effects dominate.

Adequate stimulation of various receptors in muscles never evoked effects in the VSCT neurons which could be attributed to the connection between Ib afferents and tract neurons. It is suggested that this connection is vestigial in the cat. Very strong effects are obtained on stimulation of skin receptors indicating that the VSCT forwards exteroceptive information. Strong effects are also obtained on stimulation of muscle receptors and

attributable to the connections between high threshold muscle nerve afferents and tract neurons.

The VSCT units are influenced from skin receptors of an extensive receptive field, usually including both hindlimbs, the tail, and the skin covering the pelvic girdle. The I-units are inhibited from part of the skin area of the contralateral hindlimb and usually excited from the rest of the receptive field. It is suggested that in these units the essential message is coded as inhibition of the resting discharge. The E-units receive excitatory effects from usually the whole receptive field.

In "Comments" the functional organization of the VSCT and DSCT is compared. Some new data concerning the latter tract are discussed. It is suggested that both tracts have connections with various primary afferents organized according to a common basic pattern, though marked quantitative differences in this pattern makes the VSCT a pathway for exteroceptive information and the DSCT a pathway for proprioceptive information.

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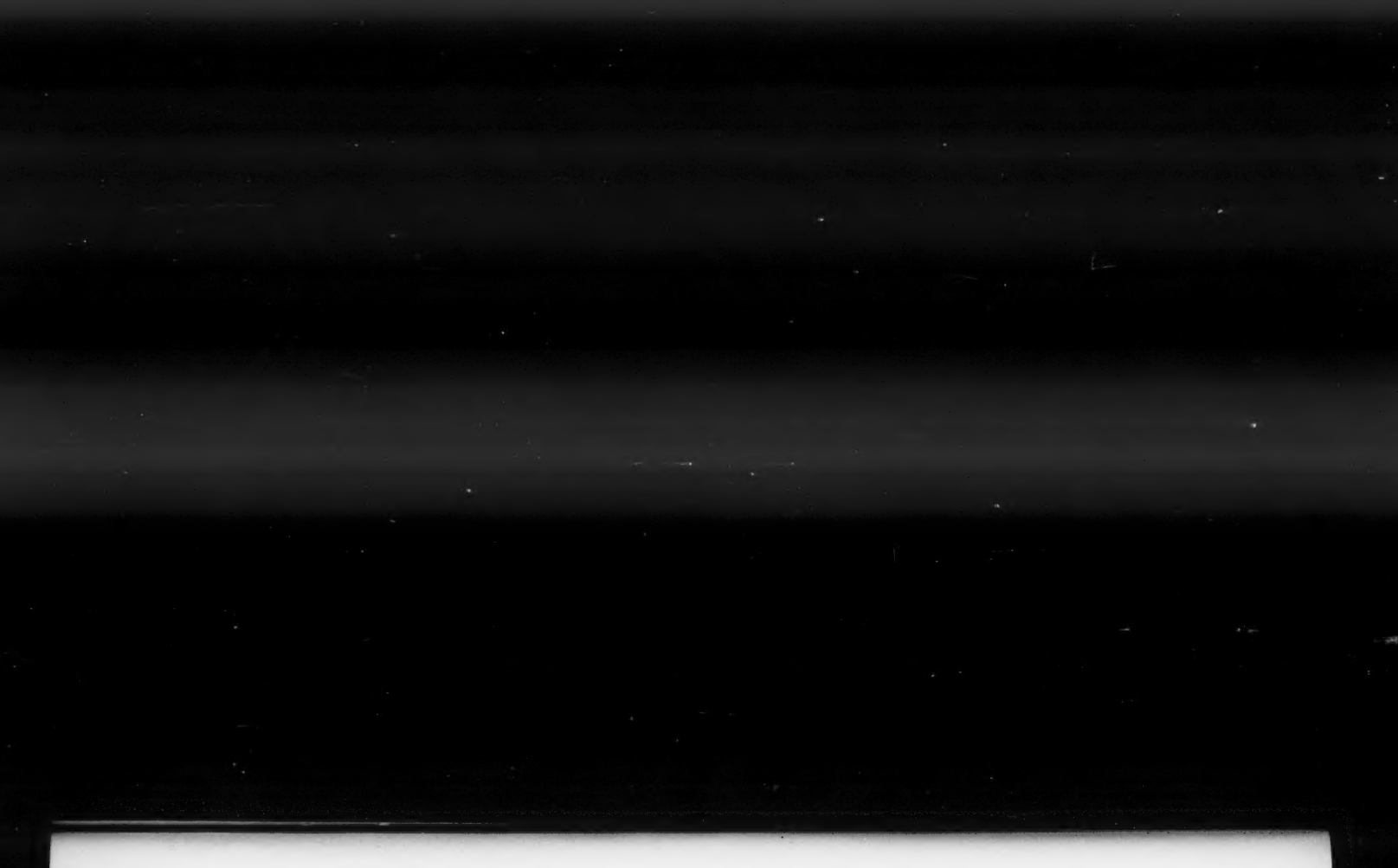
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